

THE FIRST ASIAN PLESIADAPOIDS
(MAMMALIA: PRIMATOMORPHA)

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ABSTRACT

Two new genera and species of carpolestid plesiadapoids are described from early Eocene coal beds of the Wutu Formation, Wutu Basin, Shandong Province, People's Republic of China. *Chronolestes simul*, n. gen. and sp., possesses a reduced P₃ and hypertrophied P₄ as do all carpolestids, but contrasts with other members of this family in lacking a bladelike, polycuspidate P₄. P₃₋₄ of *Chronolestes* are structurally simpler, and almost certainly more primitive, than those of any other plesiadapoid. *Chronolestes* is interpreted as the sister group of all other carpolestids and forms the basis for the new, monotypic subfamily Chronolestinae. *Carpocristes oriens*, n. gen. and sp., is a dentally derived carpolestine characterized by triple median crests on P₃₋₄ and an S-shaped blade on P₄. The closely related North American species "*Carpodaptes*" *hobackensis* and "*Carpodaptes*" *cygneus* are transferred here to the new genus *Carpocristes*. Relationships among species of *Carpocristes* are reconstructed as (*C. cygneus* (*C. hobackensis*, *C. oriens*)). Potential dental synapomorphies for Plesiadapoidea, including Plesiadapidae, Saxonellidae, and Carpolestidae, are identified for the first time. Within Plesiadapoidea, available evidence weakly supports the monophyly of a Plesiadapidae + Saxonellidae clade. *Altanius orlovi* from the early Eocene of Mongolia is unlikely to be either a plesiadapoid or a basal carpolestid.

The fossil record of North American and Asian Carpolestidae suggests at least two episodes of trans-Beringian dispersal for members of this clade during the Paleocene. The timing of these dispersal episodes is weakly constrained, but middle Torrejonian (*Chronolestes* clade) and latest Tiffanian or earliest Clarkforkian (*Carpocristes* clade) dispersal events conform with inferences regarding trans-Beringian dispersal of other groups of Paleocene mammals. The recent hypothesis that competitive exclusion by rodents may have been a causal factor underlying carpolestid extinction in North America is called into question by the co-occurrence of two carpolestids and ctenodactyloid, alagomyid, and paramyid rodents at Wutu, together with the high probability that both carpolestids and rodents coexisted in Asia through much of the Paleocene.

INTRODUCTION

Fossil placental mammals that are often referred to as "plesiadapiforms" are well known from early Cenozoic localities in North America and Europe (e.g., Russell, 1964; Rose, 1975; Gingerich, 1976; Szalay and Delson, 1979; Gunnell, 1989; Fox, 1991). Given the clear evidence for biogeographic links among early Cenozoic holarctic mammalian faunas, particularly near the Paleocene-Eocene boundary (e.g., Simpson, 1947; Dashzeveg and McKenna, 1977; Zhai, 1978; Rose, 1981; Dashzeveg, 1982, 1988; Russell and Zhai, 1987; Gingerich, 1989; Krause and Maas, 1990), the apparent absence of these forms in early Cenozoic Asian localities has been paradoxical. This absence has been particularly difficult to reconcile with phylogenetic reconstructions that ally various "plesiadapiforms" with extant colugos or dermopterans (Beard, 1993a, 1993b), which are currently endemic to parts of mainland Southeast Asia and certain islands of the southern

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Fig. 1.—Map illustrating geographic location of the Wutu Basin (star) in Shandong Province, east-central People's Republic of China.

Philippines and Sunda Shelf. Here, we partly fill a longstanding gap in the early Cenozoic fossil record of Asia by describing the first unequivocal plesiadapoids to be discovered on that continent. The specimens were collected from early Eocene coal beds belonging to the Wutu Formation in the Wutu Basin, Changle County, Shandong Province, People's Republic of China (Fig. 1).

The initial discovery of Paleogene mammals in the Wutu Basin was reported by Chow and Li (1963, 1965), who described the isctolophid perissodactyl *Homogalax wutuensis* and indeterminate pantodont remains from surface exposures of the Wutu Formation. Renewed efforts in the Wutu Basin by field crews from the Institute of Vertebrate Paleontology and Paleoanthropology (IVPP) under the leadership of Tong Yongsheng and Wang Jingwen have led to the recovery of a diversified new mammalian fauna, which includes the two carpolestid plesiadapoids described here. The new fauna is derived from coal beds that lie stratigraphically above the surface exposures that yielded the *Homogalax* fossils reported by Chow and Li (1963, 1965). The soricomorph lipotyphlan *Changlelestes dissetiformis* (Tong and Wang, 1993), *Homogalax*, a new genus and species of artiodactyl, and a diversity of rodents (Tong and Dawson, 1995), among many other taxa, are associated with the carpolestids in this new fauna.

SYSTEMATIC PALEONTOLOGY

Class Mammalia Linnaeus, 1758

Mirorder Primatomorpha Beard, 1991

Superfamily Plesiadapoidea Trouessart, 1897

Family Carpolestidae Simpson, 1935b

Subfamily Chronolestinae, **new subfamily**

Type Genus.—*Chronolestes*, n. gen.

Diagnosis.—Differs from Carpolestinae in having simpler I¹, without distoapical or mesio-basal cusps; P³⁻⁴ morphologically simple, each with only one labial cusp and lacking median crest; upper molars with little or no development of hypocone; dentary relatively longer than in Carpolestinae, especially in region of

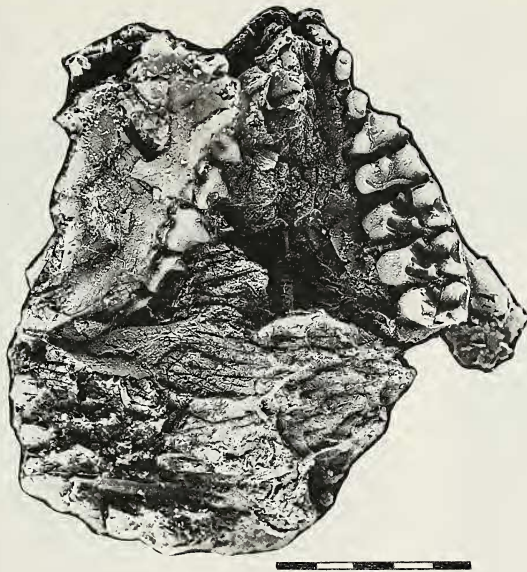


Fig. 2.—*Chronolestes simul*, n. gen. and sp., holotype (part), IVPP V10695-1. Crushed skull preserving left P¹–M³ and right P²–M². Scale = 5 mm.

I₁–P₄; P₄ hypertrophied as in Carpolestinae, but without proliferation of apical cusps forming bladeliike, plagiulacoid structure.

Chronolestes, new genus

Type Species.—*Chronolestes simul*, n. sp.

Diagnosis.—As for the subfamily (currently monotypic).

Etymology.—Greek *chronos*, time; and Greek *lestes*, robber.

Chronolestes simul, new species

(Fig. 2–8; Table 1)

Holotype.—IVPP V10695-1 (Fig. 2), crushed skull preserving left P¹–M³, right P²–M² (M³ is probably also preserved on the right side, in which case it is currently obscured by matrix), and IVPP V10695-2 (Fig. 3, 4A), associated left dentary preserving I₂–P₂ and P₄–M₃. The crushed skull and dentary were recovered from the same small block of matrix and are thought to represent the same individual, although the upper and lower jaws were not preserved in occlusion.

Hypodigm.—The holotype; IVPP V10696.1-1, left dentary preserving P₄–M₃, and IVPP V10696.1-2, associated right dentary preserving P₃–M₃ (M₂₋₃ damaged); IVPP V10696.2-1, left dentary preserving I₁₋₂ (I₂ broken), P₂–M₂ (M₂ broken), IVPP V10696.2-2 (Fig. 6C–D), associated right premaxilla/maxilla(?) preserving I¹ and ?I³, and IVPP V10696.2-3, associated right dentary preserving I₁–M₃ (Fig. 4B, 5); IVPP V10696.3-1 (Fig. 7), right maxilla preserving P²–M³, IVPP V10696.3-2 (Fig. 6A–B), associated left premaxilla/maxilla(?) preserving I¹–?I³ (I² broken); IVPP V10696.4-1, left dentary preserving P₄–M₃; IVPP V10696.4-2, left dentary preserving P₄–M₁; IVPP V10696.5-1, left dentary preserving C₁–M₃ (C₁ broken), and IVPP V10696.5-2, associated left I₁; IVPP V10696.6, left dentary preserving P₂₋₄; IVPP V10696.7, right dentary preserving M₂₋₃; IVPP 10696.8-1, left dentary

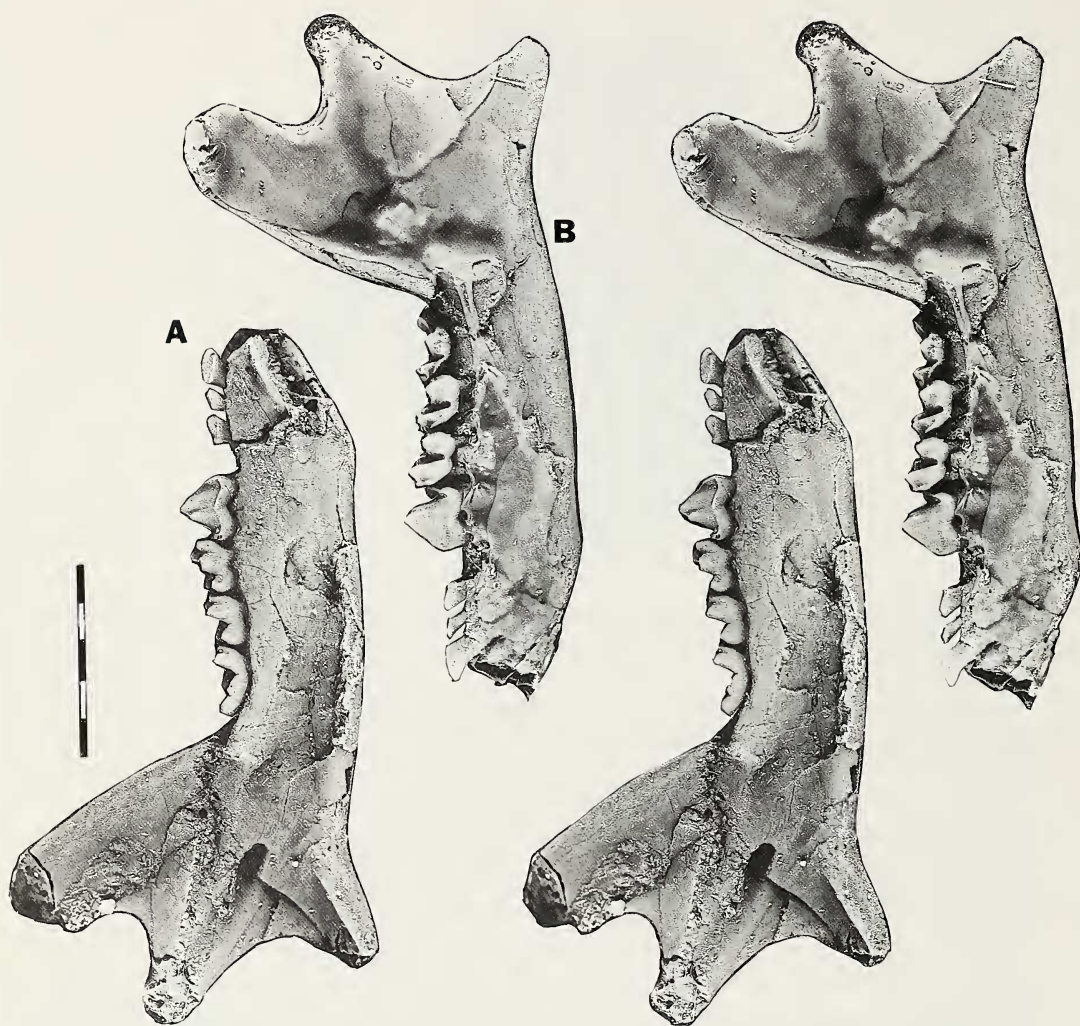


Fig. 3.—*Chronolestes simul*, n. gen. and sp., holotype (part), IVPP V10695-2. Left dentary preserving I_2 - P_2 , P_4 - M_3 , in lingual (A) and buccal (B) views (stereopairs). Scale = 5 mm.

preserving P_2 - M_2 ; IVPP V10696.8-2, isolated left M^1 ; IVPP V10696.9, right dentary preserving P_4 (broken); IVPP V10696.10, isolated left I^1 ; IVPP V10696.11 (Fig. 8), left maxilla preserving P^2 - M^3 and associated left premaxilla/maxilla(?) preserving I^1 -? I^3 ; IVPP V10696.12, left dentary preserving I_1 - M_3 ; IVPP V10696.13, right maxilla preserving P^2 - M^3 and associated left M^3 . Ambiguities concerning the homologies of anterior upper dental loci in the available sample are discussed below.

Type Locality.—County Mine, Changle County, Shandong Province, People's Republic of China. A detailed map showing the location of the County Mine with respect to the modern village of Wutu was published by Russell and Zhai (1987: fig. 36).

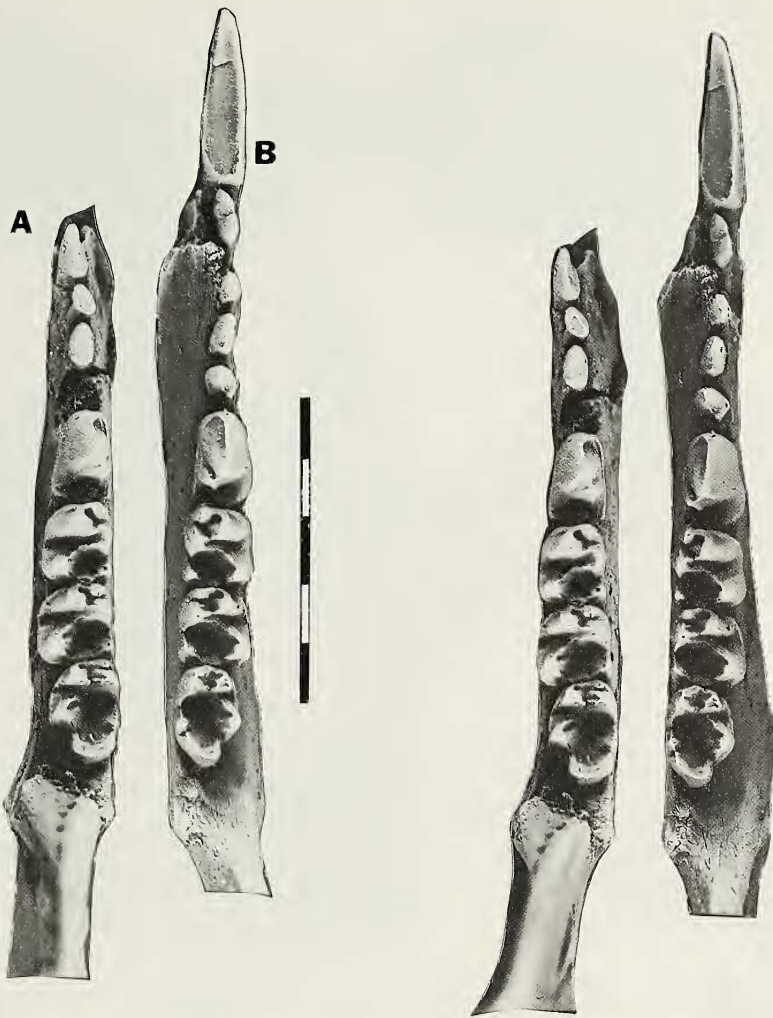


Fig. 4.—*Chronolestes simul*, n. gen. and sp. (A) IVPP V10695-2, holotype left dentary preserving I_2 – P_2 , P_4 – M_3 in occlusal view. (B) IVPP V10696.2-3, right dentary preserving complete lower dentition in occlusal view. Both views are stereopairs. Scale = 5 mm.

Known Distribution.—Early Eocene, Wutu Formation, Wutu Basin, Shandong Province, People's Republic of China.

Diagnosis.—As for the genus (currently monotypic).

Etymology.—Latin *simul*, at the same time; in allusion to the temporal coexistence of two species of carolestids at this locality.

Description.—The current hypodigm of this species includes several specimens that are extraordinarily complete, so that the entire lower dentition and possibly all of the loci comprising the upper dentition are known and identifiable. Remaining ambiguity concerning the upper dental formula of *Chronolestes simul* stems from the fact that no single specimen preserves the entire upper dentition in serial association. Dental measurements for this sample are provided in Table 1.

The lower dental formula of *Chronolestes simul* can be reasonably inferred, since all loci are represented by their crowns in IVPP V10696.2-3 and IVPP V10696.12 (Fig. 3–5). Here, the lower dental

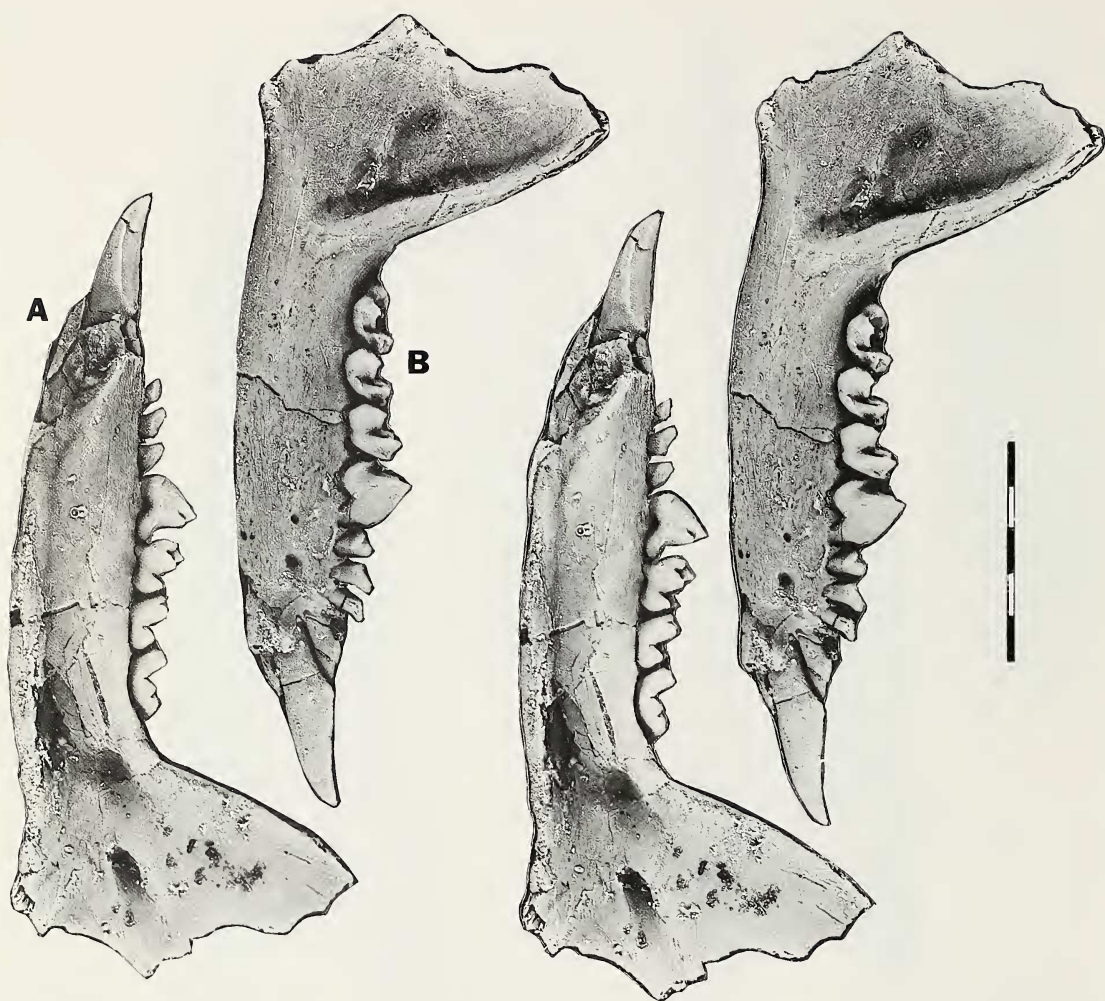


Fig. 5.—*Chronolestes simul*, n. gen. and sp., IVPP V10696.2-3. Right dentary preserving complete lower dentition in lingual (A) and buccal (B) views (stereopairs). Scale = 5 mm.

formula of *Chronolestes simul* is interpreted as 2-1-3-3, the same as that proposed by Rose (1975) for the primitive carpolestine *Elphidotarsius*, based on specimens of *Elphidotarsius* sp., cf. *E. florencae*. A second species of *Elphidotarsius*, *E. shotgunensis*, appears to have possessed a more primitive lower dental formula of 3-1-3-3 (Gazin, 1971; Fox, 1993). If so, the similarly derived lower dental formula in *Chronolestes simul* and *Elphidotarsius* sp., cf. *E. florencae* is the product of convergence.

As in all plesiadapoids, I_1 in *Chronolestes simul* is an enlarged, procumbent tooth. Its crown is elongated and relatively slender, resembling I_1 in *Carpodaptus* and *Carpolestes* more than the shorter and stouter I_1 found in *Elphidotarsius* (see Rose, 1975:fig. 5). As is the case in most carpolestids, there is no development of a basal cusp on the lingual cingulid of I_1 in *Chronolestes*, in contrast to the condition in *Elphidotarsius wightoni* and plesiadapids.

Prior to this report, the crown of I_2 has not been described in any carpolestid. In *Chronolestes* this tooth resembles I_1 in being procumbent and in having an elliptical, semilanceolate crown. Nevertheless, as would be expected from alveoli for these teeth in other carpolestid taxa, I_2 is much smaller than I_1 .

The smallest of the lower teeth in *Chronolestes* is interpreted as C_1 , in contrast to the situation in *Elphidotarsius* sp., cf. *E. florencae*, in which P_2 is likely smaller than C_1 (as judged from their alveoli).

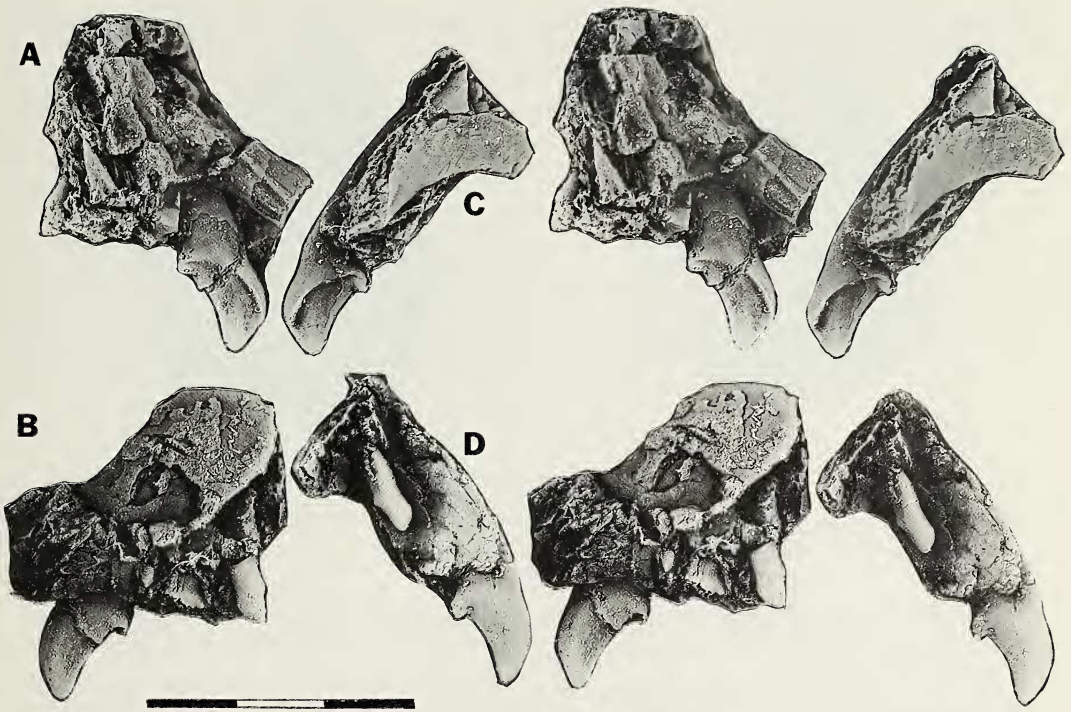


Fig. 6.—*Chronolestes simul*, n. gen. and sp. (A–B) IVPP V10696.3-2, left premaxilla/maxilla(?) preserving I¹–?I³ (I² broken) in lingual (A) and labial (B) views. Note that the ostensible presence of two basal cusps on I¹ in this specimen is an artifact caused by breakage; see the undistorted crown preserved in IVPP V10696.2-2. (C–D) IVPP V10696.2-2, right premaxilla/maxilla(?) preserving I¹ and ?I² in lingual (C) and labial (D) views. All views are stereopairs. Scale = 5 mm.

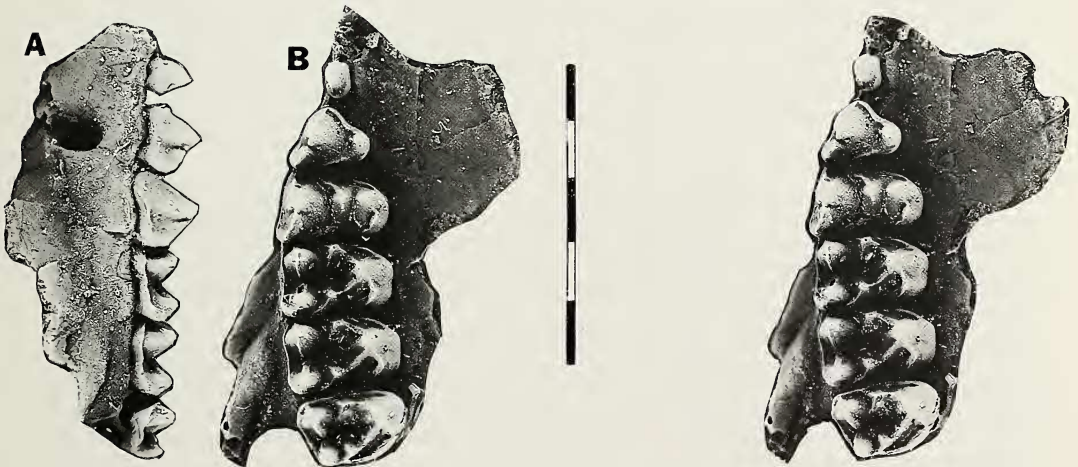


Fig. 7.—*Chronolestes simul*, n. gen. and sp., IVPP V10696.3-1. Left maxilla preserving P²–M³ in buccal (A) and occlusal (B) views. Occlusal view is stereopair. Scale = 5 mm.

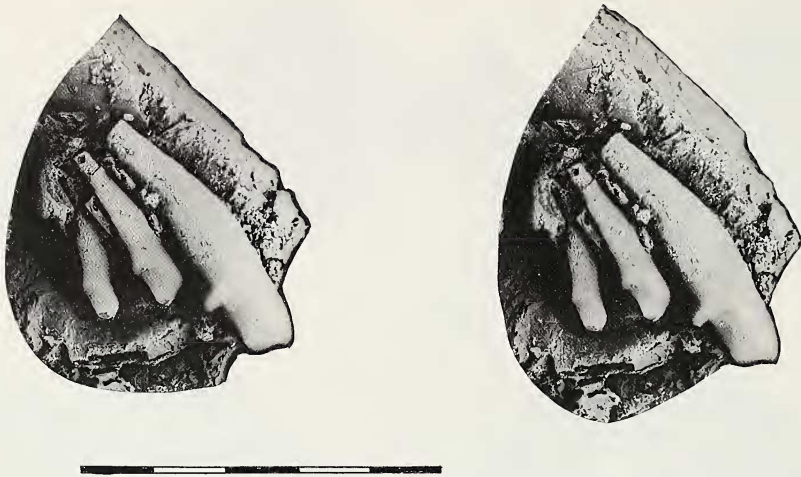


Fig. 8.—*Chronolestes simul*, n. gen. and sp., IVPP V10696.11. Left premaxilla/maxilla(?) preserving I¹–I³ in lingual view (stereopair). Scale = 5 mm.

The crown of C_1 is very simple or even vestigial in morphology, consisting solely of an anteriorly canting cusp. In overall morphology, this tooth closely resembles C_1 in *Elphidotarsius wightoni* and *Pronothodectes matthewi*.

The crown of P_2 has not been described previously in any carpolestid. As noted earlier, P_2 is larger than C_1 , from which it also differs in having a weakly defined talonid heel in addition to the anteriorly canting protoconid. P_2 in *Chronolestes* is very similar in overall morphology to that of *Pronothodectes matthewi*, thus providing further evidence for the plesiadapoid affinities of the Carpolestidae.

P_3 is single-rooted in all specimens of *Chronolestes* in which the crown of this tooth is preserved ($n = 6$). This derived feature was apparently attained convergently in *Chronolestes* and advanced carpolestines, because *Elphidotarsius* sp., cf. *E. florencae* retains two closely appressed roots on this tooth and is relatively larger (Rose, 1975). In structure, P_3 closely resembles P_2 , from which it differs primarily in being slightly larger (except in IVPP V10696.6, in which $P_2 > P_3$) and relatively wider, with a more robust root. As is the case in all carpolestids for which this tooth is known, P_3 is greatly reduced in comparison with P_4 .

Because of the unique specializations of P_4 in carpolestids, the anatomy of this tooth has proven especially useful in assessing relationships within the group (e.g., Rose, 1975; Krause, 1978; Fox, 1984b). This is particularly true in the case of *Chronolestes*. P_4 in *Chronolestes* is hypertrophied as in other carpolestids, yet it lacks development of a polycuspidate, plagiaulacoid or bladeliike crown morphology (Fig. 9). The trigonid bears only two cusps, the protoconid and metaconid. The protoconid occupies the apex of the crown. The leading or anterior margin of the crown is marked by a weak crest that runs anteriorly and inferiorly from the apex of the protoconid to near the base of the crown, where it is lingually continuous with a variably developed cingulid. The metaconid is much smaller than the protoconid and is positioned lingual and posterior to it. A crest unites the apices of the metaconid and protoconid. A second crest runs inferiorly from the metaconid to join an anteriorly directed crest from the single talonid cusp. The talonid heel is anteroposteriorly longer and more prominently developed than in carpolestines. Its labial border is marked by a relatively deeply invaginated hypoflexid. P_4 in *Chronolestes* is moderately exodaenodont, with swollen bulges of enamel overlapping its roots labially.

The lower molars of *Chronolestes* generally resemble those of primitive carpolestines, especially *Elphidotarsius florencae*. Nevertheless, in several respects the lower molars of *Chronolestes* differ from those of most or all other carpolestids. In practically all of these cases, *Chronolestes* appears to have retained more primitive lower molar characters than did carpolestines, because the lower molars of *Chronolestes* more closely approximate conditions seen in other primitive plesiadapoids, such as *Pronothodectes* and *Saxonella*.

The paraconid of M_1 in *Chronolestes* is situated lingually and is not strongly splayed anteriorly with respect to the metaconid. In this primitive feature *Chronolestes* resembles *E. florencae* but differs from other species of *Elphidotarsius* and more advanced carpolestines. In contrast to all carpolestines, the

Table 1.—Summary of dental measurements (in mm) for the sample of *Chronolestes simul* reported here. Abbreviations: n, sample size; OR, observed range; SD, standard deviation; CV, coefficient of variation.

Tooth	n	OR	Mean	SD	CV
I ₁ , length	4	2.75–3.10	2.94	0.14	4.89
I ₁ , width	4	0.65–0.85	0.80	0.10	12.50
I ₂ , length	3	0.85–0.95	0.90	0.05	5.56
I ₂ , width	3	0.40–0.45	0.43	0.03	6.66
C ₁ , length	3	0.50–0.55	0.53	0.03	5.41
C ₁ , width	3	0.40	0.40	0	0
P ₂ , length	7	0.60–0.75	0.66	0.06	8.38
P ₂ , width	7	0.35–0.50	0.43	0.06	14.84
P ₃ , length	7	0.50–0.70	0.61	0.07	12.18
P ₃ , width	7	0.45–0.65	0.54	0.07	12.88
P ₄ , length	11	1.45–1.80	1.67	0.10	6.18
P ₄ , width	11	0.90–1.15	1.02	0.08	7.69
M ₁ , length	10	1.30–1.55	1.42	0.07	5.28
M ₁ , width	10	1.10–1.30	1.22	0.07	5.53
M ₂ , length	8	1.30–1.50	1.41	0.07	5.18
M ₂ , width	8	1.20–1.45	1.30	0.08	6.50
M ₃ , length	7	1.70–1.90	1.77	0.08	4.27
M ₃ , width	7	1.15–1.30	1.21	0.04	3.73
I ¹ , length	3	1.10–1.25	1.17	0.08	6.55
I ¹ , width	3	0.75–0.85	0.78	0.06	7.37
I ² , length	1	0.75	0.75	—	—
I ² , width	1	0.40	0.40	—	—
I ³ , length	2	0.50–0.60	0.55	—	—
I ³ , width	2	0.25–0.35	0.30	—	—
P ¹ , length	1	0.75	0.75	—	—
P ¹ , width	1	0.45	0.45	—	—
P ² , length	4	0.55–0.70	0.63	0.06	10.33
P ² , width	4	0.40–0.50	0.46	0.05	10.35
P ³ , length	4	1.05–1.30	1.16	0.13	11.31
P ³ , width	4	1.10–1.40	1.25	0.12	9.80
P ⁴ , length	4	1.10–1.35	1.24	0.11	8.96
P ⁴ , width	4	1.85–2.05	1.93	0.10	4.97
M ¹ , length	5	1.30–1.40	1.34	0.04	3.12
M ¹ , width	5	1.80–2.20	2.04	0.16	7.63
M ² , length	4	1.10–1.35	1.23	0.12	9.72
M ² , width	4	2.05–2.20	2.11	0.08	3.55
M ³ , length	5	1.10–1.20	1.17	0.04	3.82
M ³ , width	5	1.80–1.95	1.85	0.07	3.82

metaconid of M₁ is situated only slightly posterior to the level of the protoconid, the M₁ talonid is relatively unreduced in its anteroposterior dimension, and a comparatively well-developed hypoconulid occurs on the central part of the posteristid. The cristid obliqua runs anterolingually up the postvallid to join the metaconid, as is typical for carpolestids. The talonid notch is less apparent than is the case in carpolestines, and the ectocingulid is variably, but always weakly, developed.

M₂₋₃ in *Chronolestes* more closely resemble these teeth in carpolestines than does M₁, but some fairly subtle differences remain. The talonid of M₂ is relatively longer, and the crown as a whole leans less in the lingual direction than is the case in many carpolestines (e.g., *Elphidotarsius* sp., cf. *E. florencae*, *E. wightoni*, *E. russelli*). As in M₁, M₂ bears a conspicuous hypoconulid and lacks the strongly developed talonid notch found in most carpolestines. The talonid of M₃ is relatively wider than is typical in *Elphidotarsius*.

As noted in the subfamilial diagnosis, the dentary of *Chronolestes* is unique among carpolestids in showing greater anterior elongation than occurs in carpolestines. In conjunction with progressive hypertrophy of I₁ and P₄, loss of P₂, and reduction in size of P₃, the dentary became increasingly foreshortened in advanced carpolestines (Rose, 1975). Accordingly, the anterior elongation of the

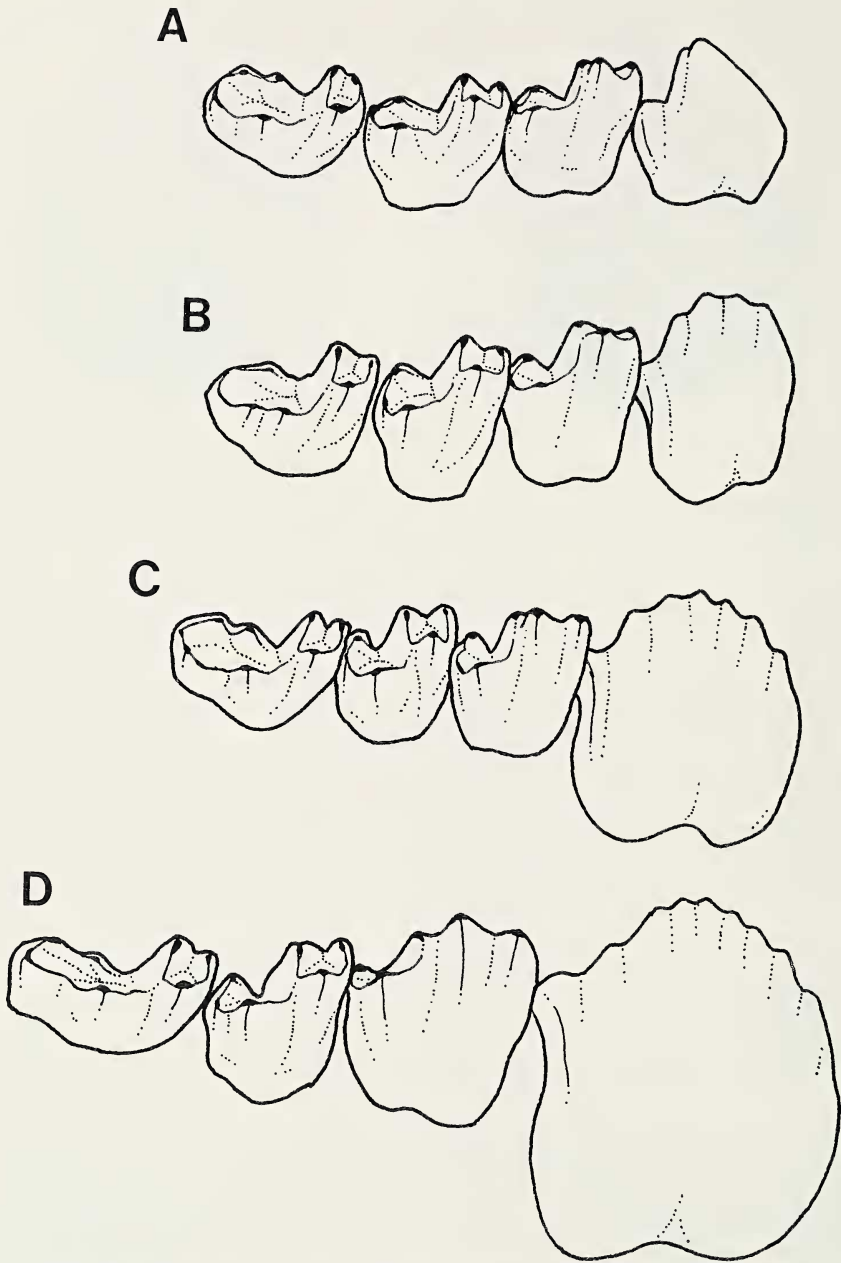


Fig. 9.—Lower cheek teeth of selected carpolestids in buccal view, drawn at the same scale (modified after Rose, 1975:fig. 34). (A) *Chronolestes simul*; (B) *Elphidotarsius* sp., cf. *E. florencae*; (C) *Carpodaptus hazelae*; (D) *Carpolestes dubius*. The sequence from A–D likely corresponds to a morphocline in terms of (a) progressive hypertrophy of P_4 ; (b) development of polycuspidate, bladelike P_4 crown morphology; and (c) mesiodistal splaying of M_1 trigonid so that M_1 paraconid, paracristid, and protoconid become functionally incorporated into P_4 shearing blade.

dentary in *Chronolestes* can be identified as a primitive retention, reflecting its relatively unspecialized degree of anterior dental reduction and plagiaulacoid adaptations (Simpson, 1933). Also in contrast to advanced carpolestines, in which the dentary became progressively deeper to accommodate the large, bladellike P₄, the dentary of *Chronolestes* is relatively shallow (2.55 mm beneath P₄ in IVPP V10696.1-1). In other respects the dentary of *Chronolestes* does not depart from conditions described in other carpolestids by Rose (1975:54).

Parts of the anterior upper dentition of *Chronolestes simul* are preserved in three specimens, IVPP V10696.2-2, IVPP V10696.3-2, and IVPP V10696.11 (Fig. 6, 8). The most nearly complete of these is IVPP V10696.11, a fragment of left premaxilla and (possibly) maxilla bearing the crowns of the three anteriormost teeth. The three anteriormost crowns preserved in IVPP V10696.11 generally resemble the teeth occupying the same positions in *Carpolestes nigridentis*, which is the only other carpolestid in which these teeth have been described or illustrated in situ (see Rose, 1981:62–63; Gingerich, 1987:fig. 6). Traditionally, the homologies of these loci in *Carpolestes nigridentis* have been interpreted as I¹, I², and C¹ (e.g., Rose, 1981), but Fox (1984b, 1993) has made a compelling case that the posteriormost of these loci actually represents I³ rather than C¹. If Fox's interpretation is correct, it is likely that the three anteriormost crowns preserved in IVPP V10696.11 also represent I¹⁻³. Knowledge of the position of the premaxillary–maxillary suture in *Chronolestes simul* is necessary to confirm its upper dental formula, but available specimens are not sufficiently preserved to show this feature.

I¹ is an enlarged and highly diagnostic tooth in all plesiadapoids and their close relatives (e.g., Rose et al., 1993), and there can be no doubt that the anteriormost crown preserved in IVPP V10696.11, IVPP V10696.2-2, and IVPP V10696.3-2 represents this locus (also preserved in IVPP V10696.10). I¹ in *Chronolestes simul* is most notable for its simplicity. In this respect the tooth contrasts markedly with I¹ in carpolestines (currently known in *Carpodaptes hazelae*, "*Carpodaptes*" *cygneus* and *Carpolestes* sp., cf. *C. nigridentis*; see Krause, 1978; Fox, 1984b, 1993; Gingerich, 1987). The crown as a whole is recurved and dominated by a single apical cusp, which apparently corresponds with the mesio-apical cusp or anterocone on I¹ in carpolestines. A mesial crest connects the apex of the anterocone with a well-developed and continuous lingual cingulum. Neither a laterocone nor a mediocone is present. A distal crest unites the apex of the anterocone with a much smaller basal cusp, which seems to be homologous with the disto-basal cusp or posterocone on I¹ in carpolestines. There is no mesio-basal cusp.

The simple I¹ morphology found in *Chronolestes* exceeds that seen in the micromomyid *Tinimomys* (Rose et al., 1993), but is structurally very close to an isolated I¹ (University of Minnesota 2194) from the late Puercan of Montana which forms part of the hypodigm of a new genus and species of plesiadapoid being described by Van Valen (in press). The similar I¹ structure found in *Chronolestes* and Van Valen's new Puercan plesiadapoid likely reflects the morphotypic condition for Plesiadapoidea, on the basis of (1) the great age of Van Valen's new genus; (2) the simple (and thus plausibly primitive) structure of I¹ in *Chronolestes* and Van Valen's new plesiadapoid; (3) the relatively basal phylogenetic positions of *Chronolestes* and Van Valen's new plesiadapoid with respect to the plesiadapoid radiation; and (4) the slightly more complicated I¹ morphology found in *Tinimomys*, a genus that seems to lie outside of Plesiadapoidea (Beard, 1993a, 1993b), but which may have retained a relatively simple I¹ that was altered little from the plesiadapoid morphotype. If the simple structure of I¹ shared by *Chronolestes*, Van Valen's new plesiadapoid, and *Tinimomys* is the result of sympleiomorphy (as seems likely), it follows that the more complicated I¹ crowns found in many plesiadapoid, carpolestid, saxonellid, and paromomyid genera are not entirely homologous, especially from family to family (contra Gingerich, 1976:89; Krause, 1978:1255; Rose et al., 1993). A similar conclusion was reached by Fox (1991:340–341) on the basis of his reconstruction of the evolution of the upper and lower central incisors of saxonellids. Krause's (1978:1255) hypothesis that the disto-apical cusp of carpolestine I¹s is "probably homologous" with the laterocone of plesiadapoid I¹s (see also Gingerich, 1976; Rose et al., 1993) is incompatible with our reconstruction of the evolution of the I¹s among Plesiadapoidea and can be refuted if our character walk ultimately proves to be accurate.

I² is preserved in IVPP V10696.11. This tooth in *Chronolestes simul* is morphologically very similar to I² in *Carpolestes nigridentis*, which is the only other carpolestid for which this crown has been described or illustrated [Rose, 1981:fig. 27; Gingerich, 1987:fig. 6 (the specimen illustrated by Gingerich was referred by him to *Carpolestes* sp., cf. *C. nigridentis*)]. The crown is dominated by a single mesially-canted cusp showing only slight apical wear. The light wear on I² is remarkable because I¹ in the same specimen shows very heavy apical wear, with no remaining trace of the anterocone as a distinct cusp. As a whole, I² is notably asymmetrical. The primary cusp possesses a short, weakly inclined mesial surface that contrasts with its longer, more steeply sloped distal surface. There is variable development of a secondary, distobasal cusp on I² in *Chronolestes simul* (absent in IVPP V10696.11, conspicuous

in IVPP V10696.3-2). The root of I² is strongly elliptical in cross section, being longer mesiodistally than labiolingually.

I³(?) is much smaller and morphologically simpler than I². As in *Carpolestes nigridentis*, I³ in *Chronolestes simul* bears a single cusp that is slightly canted mesially. Overall, the crown is more symmetrical than that of I², and the tooth bears a root that is nearly circular in cross section.

The most nearly complete, serially associated upper dentition currently known for *Chronolestes simul* is preserved in the holotype crushed skull, IVPP V10695-1 (Fig. 2). This specimen preserves the crowns of seven maxillary teeth on the left side, interpreted here as P¹-M³. Anterior to the crown interpreted as P¹ the maxilla is badly fractured and distorted, precluding determination of whether or not an additional maxillary alveolus (for C¹) was present. Nevertheless, it appears that the maxilla would have extended an appreciable distance anterior to the level of P¹. This observation and those of Fox (1984b, 1993) concerning the upper dental formula in primitive carpoolestines support identification of the anteriormost crown on the left side of IVPP V10695-1 as P¹ rather than C¹.

P¹ in *Chronolestes simul* is simple in morphology, being dominated by a single, anteriorly-placed cusp, which is broken in IVPP V10695-1, followed by a weak heel. The crown as a whole is more elongated anteroposteriorly and is supported by a root having a much more elliptical cross section than is the case in *Elphidotarsius wightoni* and *Carpodaptes hazelae*, the only other carpoolestids for which this tooth has been described (Simpson, 1937; Fox, 1984b). Also in contrast to both of the latter species, P¹ lacks a lingual cingulum in *Chronolestes simul*.

P² is separated from P¹ by a short diastema, in contrast to the condition in such primitive carpoolestines as *Elphidotarsius wightoni* and *Carpodaptes hazelae*, in which this diastema is absent (Fox, 1984b). In the holotype skull, P² appears to be double-rooted, but in other specimens (e.g., IVPP V10696.11) these roots seem to have coalesced. A double-rooted P² has never been described in carpoolestines, but this condition is known to occur in certain other plesiadapoids, such as *Saxonella naylori* (Fox, 1991) and *Pronothodectes matthewi* (Gingerich, 1976). Like that of P¹, the crown of P² in *Chronolestes* is simple, bearing a single primary cusp followed by a low heel. The primary cusp is more centrally positioned on P² than on P¹, giving the crown a more symmetrical appearance in occlusal view. Lingually, there is only weak development of a cingulum.

P³⁻⁴ show striking morphologic specializations among carpoolestines (Rose, 1975; also see below) that contrast markedly with the simpler, more primitive conditions found in *Chronolestes*. P³ in *Chronolestes simul* is roughly triangular in occlusal outline, being much longer labially than lingually. Its crown bears only two cusps: a relatively large paracone positioned about midway along the labial border of the tooth, and a much smaller protocone occupying the anterior margin of the modest lingual lobe. The anterior border of the paracone is smoothly convex, but the posterior border is marked by a prominent crest that runs from the apex of the paracone to the posterolabial margin of the tooth. The posterior part of the latter structure shows only slight swelling in the region where a distinct metacone occurs in *Elphidotarsius* sp., cf. *E. florencae* and all other carpoolestines (Rose, 1975). A simple valley or crease separates the bases of the paracone and protocone. There is no development of an intervening conule or its associated median crest, in contrast to conditions in Saxonellidae, Plesiadapidae, and Carpolestinae. Modest pre- and postcingula line the anterior and posterior margins of the tooth.

Overall, P³ in *Chronolestes simul* is structurally more primitive than that of any other plesiadapoid: a distinct metacone and paraconule occur on P³ in *Pronothodectes* and the P³ of *Saxonella*, while also bearing these structures, is dramatically specialized in its own way (Fox, 1991). Among carpoolestines, P³ is uniformly more specialized than is the case in *Chronolestes simul*. The most primitive carpoolestine for which P³ has been described is *Elphidotarsius* sp., cf. *E. florencae*, but even in this species P³ bears a well-developed metacone and possesses a median crest and associated cusp. The simpler structure of P³ in *Chronolestes simul* therefore lends credence to Rose's view concerning the primitive nature of P³ in *Elphidotarsius* sp., cf. *E. florencae*, relative to that of *Pronothodectes*: "P³ in the former [*Elphidotarsius* sp., cf. *E. florencae*], however, is not divided into three longitudinal parts, as in *Pronothodectes* (and later carpoolestids). The simpler P³, like that of *Elphidotarsius*, was probably the ancestral condition" (Rose, 1975:63).

P⁴ in *Chronolestes*, like P³, is morphologically simpler than that of any other plesiadapoid. Its crown is nearly trapezoidal in occlusal view, being much wider (transversely) than long. The labial border of the tooth is marked by a single cusp, the paracone, which is the largest cusp on P⁴. Anterior and posterior crests run from the apex of the paracone toward the base of the crown. Of these, the posterior crest is the more trenchant and terminates higher on the crown. As in P³, there is no development of a metacone on the posterior crest. Immediately lingual and slightly anterior to the midline of the paracone is a distinct paraconule. A preparaconule crista arcs anteriorly from the paraconule to become continuous with the anterior crest from the paracone at the anterolabial border of the tooth. The

smallest cusp on P^4 is the protocone, which lies directly lingual to the paraconule. A short precingulum lines the base of the crown anterior to the paraconule and protocone. A much more extensive postcingulum runs continuously from the base of the protocone to the posterolabial corner of the tooth. A weak swelling occurs at the lingual end of the postcingulum, but this structure is too weak to be called a small hypocone.

In overall structure, P^4 in *Chronolestes simul* closely resembles that in *Pronothodectes matthewi*, from which it differs in lacking development of a metacone and in having a protocone that is smaller and less projecting relative to the paraconule. In the most primitive carpolestine for which P^4 has been described, *Elphidotarsius* sp., cf. *E. florencae*, this tooth is considerably more specialized than that of *Chronolestes simul* in bearing four labial cusps, a well-developed median crest consisting of pre- and postparaconule cristae as well as the paraconule, and more elaborate pre- and postcingula.

The upper molars of *Chronolestes* do not differ markedly from those of carpolestines, especially those of such primitive taxa as *Elphidotarsius* sp., cf. *E. florencae*. The upper molars of *Chronolestes* differ modestly from those of carpolestines in lacking distinct hypocones and in having less pronounced development of conules and their associated crests. The upper molars of *Chronolestes* further differ from those of *Elphidotarsius* sp., cf. *E. florencae* and other primitive carpolestines in being less transverse and in having the paracone and metacone more widely separated. Interestingly, the upper molars of the derived carpolestine *Carpolestes* approach those of *Chronolestes* in this respect. Outside of the Carpolestidae, a particularly close approximation of the upper molar morphology of *Chronolestes* is found in *Saxonella*.

Discussion.—Given its relatively late temporal occurrence, *Chronolestes simul* retains a surprisingly primitive dental morphology in conjunction with relatively few species-specific autapomorphies. In only two minor characters is *Chronolestes* derived with respect to conditions observed in primitive carpolestines (i.e., *Elphidotarsius* spp.): loss of I_3 (if *E. shotgunensis* did indeed retain this tooth; see Gazin, 1971; Fox, 1993) and presence of a single-rooted P_3 . Despite these relatively trivial autapomorphies, the dentition as a whole of *Chronolestes* (particularly P_4 , I^1 , and P^{3-4}) is most notable for its simple morphology, which apparently reflects its retention of numerous primitive character states. For example, P_4 in *Chronolestes* possesses only two trigonid cusps, identified above as protoconid and metaconid. In *Elphidotarsius florencae*, the most primitive carpolestine discovered to date, P_4 bears four trigonid cusps, the two anteriormost of which are seemingly lacking in *Chronolestes*. Rose (1975:16) considered the two anterior cusps on the trigonid of P_4 in *Elphidotarsius florencae* as probable homologues of the paraconid and an accessory, neomorphic cusp (from distal to mesial, respectively), but the absence of these cusps on the P_4 of *Chronolestes* suggests that both cusps are likely to be neomorphic in *Elphidotarsius* and other carpolestines. Outgroup comparisons reinforce our conclusion that paraconids were absent on P_4 in basal carpolestids (and probably in basal plesiadapoids), because this cusp is also absent on P_4 in *Pronothodectes*, *Paromomys*, *Micromomys*, and (variably) *Saxonella*, among other taxa.

In light of its distinctly primitive dental morphology, it is safe to conclude that discovery of *Chronolestes* in strata of middle Torrejonian or earlier age (or their Asian equivalents) would have conformed more with the pattern of stratigraphic distribution of carpolestids seen in North America (e.g., Rose, 1975, 1977; Archibald et al., 1987). The fact that *Chronolestes* and carpolestines cannot have shared common ancestry more recently than the middle Torrejonian reveals the existence of a hitherto unknown clade of primitive carpolestids, the Chronolestinae, from at least the middle Paleocene to the early Eocene, an interval of perhaps 7 Ma (Archibald et al., 1987). Recognition of this clade at the level of subfamily is justified on the basis of its basal phylogenetic position within the family and its long, yet poorly documented, temporal persistence.

Subfamily Carpolestinae Simpson, 1935b

Type Genus. — *Carpolestes* Simpson, 1928.

Included Genera. — *Carpodaptus* Matthew and Granger, 1921; *Elphidotarsius* Gidley, 1923; *Carpolestes* Simpson, 1928; *Carpocristes*, n. gen.

Emended Diagnosis. — Differs from Chronolestinae in having more complicated I^1 , with distinct cusps occupying at least mesio-apical, disto-apical, mesio-basal, and disto-basal positions; P^3 with at least two buccal cusps and a median crest confluent with paraconule; P^4 with at least four buccal cusps and complete median crest; M^{1-2} with at least weak development of hypocone; dentary relatively shorter than in Chronolestinae, especially in region of I_1 – P_4 ; P_4 hypertrophied, polycuspidate, and plagiaulacoid.

Discussion. — Aside from the addition of the new genus *Carpocristes*, the content of the subfamily Carpolestinae of this paper is equivalent to that of the family Carpolestidae of most previous authors (e.g., Simpson, 1935b; Rose, 1975; Szalay and Delson, 1979). Notably, Russell (1964:127) used the subfamily Carpolestinae to accommodate the same assemblage of taxa (minus *Carpocristes*, which was unknown at the time) advocated here, in order to distinguish this clade from *Saxonella*, which he also referred to the Carpolestidae. Subsequent workers have generally agreed that *Saxonella* should be classified in a family distinct from the Carpolestidae (Van Valen, 1969; Szalay, 1972; Rose, 1975; Szalay and Delson, 1979; Fox, 1991), often citing the likelihood of a closer relationship between *Saxonella* and plesiadapids than between the former genus and carpolestids. For reasons parallel to those of Russell (1964), we revive his concept of the Carpolestinae here, in order to distinguish this clade from the basal carpolestid *Chronolestes*.

Carpocristes, new genus

Type Species. — *Carpocristes oriens*, n. sp.

Included Species. — *Carpocristes oriens*, n. sp.; *Carpocristes hobackensis* (Dorr, 1952), n. comb.; *Carpocristes cygneus* (Russell, 1967), n. comb.

Diagnosis. — Differs from other carpolestines in having greater proliferation of crests comprising the median row on P^{3-4} , in having smaller molars, and in having posterior apical cusp on P_4 more posterior in position (roughly equidistant between penultimate apical cusp and talonid cusp). Further differs from *Carpolestes* in lacking pronounced anterolabial spur on P^3 , and in having P^{3-4} subequal in size. Further differs from carpolestines other than *Carpolestes dubius* in having pronounced posterolingual excavation on P_4 .

Etymology. — Greek *karpos*, fruit; and Latin *cristatus*, crested.

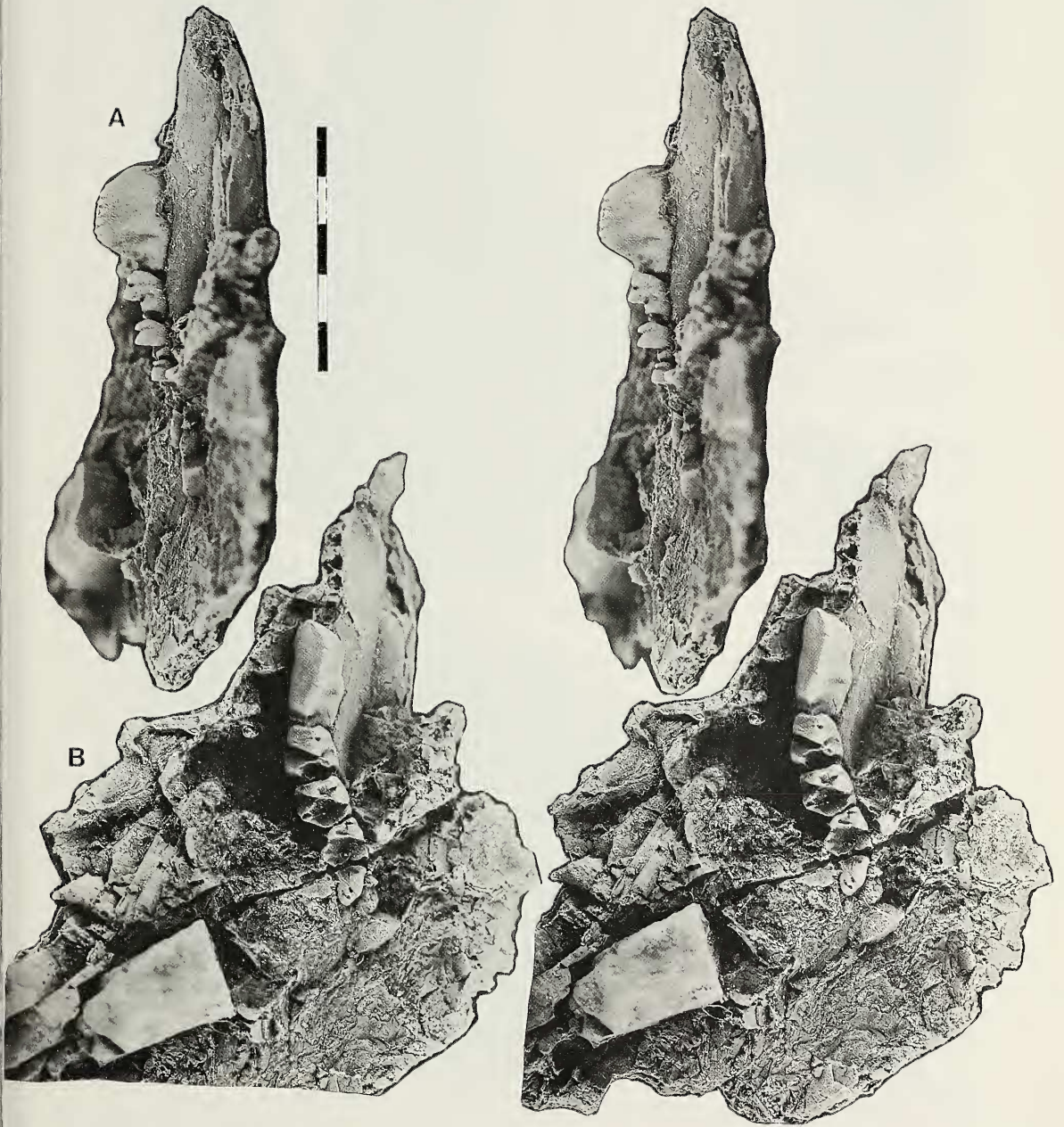
Carpocristes oriens, new species

(Fig. 10–12)

Holotype. — IVPP V10697.1-1, left dentary fragment preserving P_4 – M_3 and alveoli for anterior teeth (Fig. 10), and IVPP V10697.1-2, associated, crushed snout

→

Fig. 10. — *Carpocristes oriens*, n. gen. and sp., holotype (part), IVPP V10697.1-1. Left dentary fragment preserving P_4 – M_3 and alveoli for anterior teeth in (A) lingual and (B) occlusal views. Both views are stereopairs. Scale = 5 mm. The holotype dentary is preserved on the same small block and in near occlusion with the left maxilla and other elements representing the same individual; see Fig. 11.



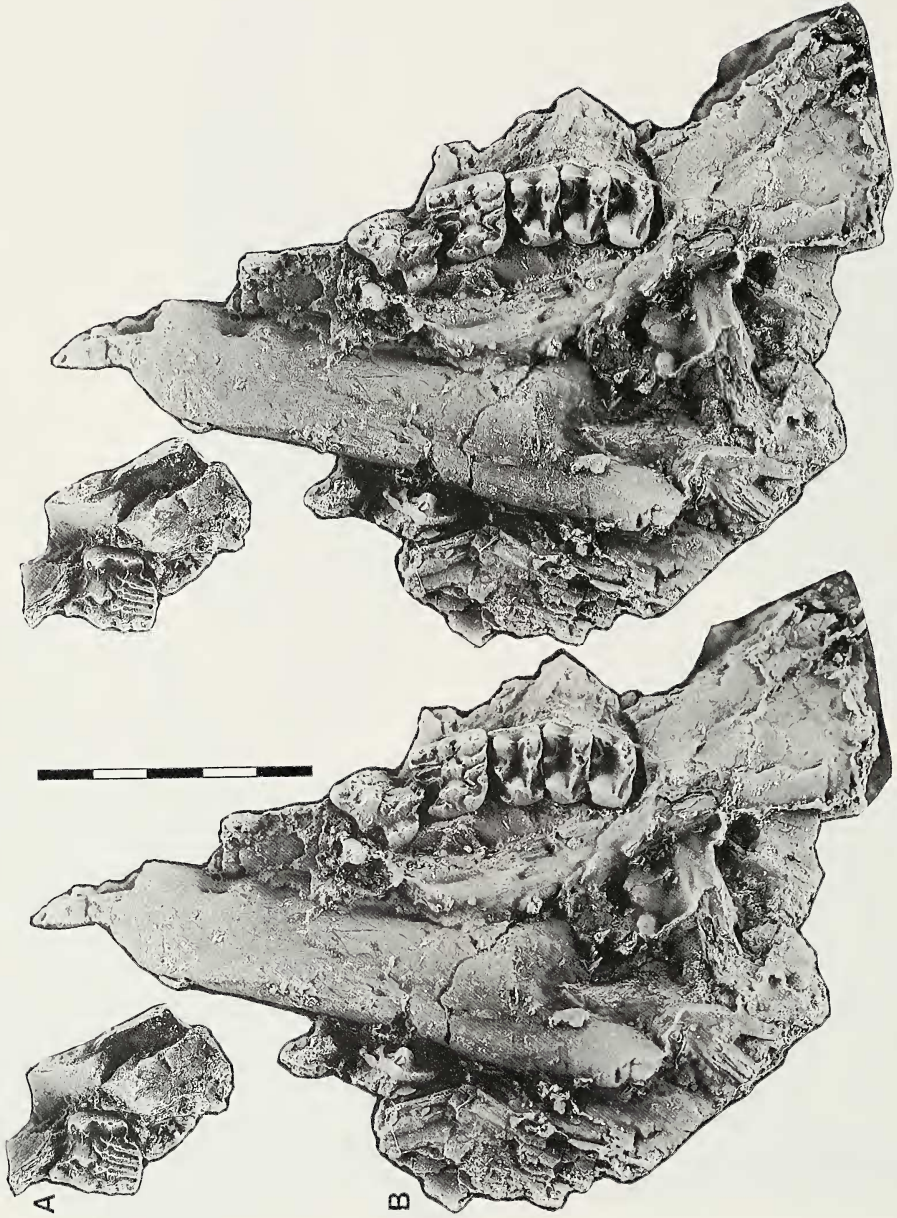




Fig. 12.—*Carpocristes oriens*, n. gen. and sp., IVPP V10697.2. Right maxilla preserving P³–M³ (anterolabial corner of P³ and lingual parts of M¹⁻² missing) in (A) buccal and (B) occlusal views. Occlusal view is stereopair. Scale = 5 mm.

preserving left P³–M³ (P³ broken), complete right P³, and unidentifiable right upper molars (Fig. 11). The dentary and snout are preserved in near occlusion and certainly represent a single individual.

Hypodigm.—The holotype; IVPP V10697.2, right maxilla fragment preserving P³–M³ (anterolabial corner of P³ and lingual parts of M¹⁻² broken; Fig. 12); and IVPP V10697.3, right maxilla fragment preserving damaged P³⁻⁴.

Type Locality.—County Mine, Changle County, Shandong Province, People's Republic of China. For detailed information concerning the geographic position of the County Mine, see Russell and Zhai (1987:fig. 36).

Known Distribution.—Early Eocene, Wutu Formation, Wutu Basin, Shandong Province, People's Republic of China.

Diagnosis.—Slightly smaller than *C. cygneus* and *C. hobackensis*. Dentary with four, rather than three, alveoli between I₁ and P₄, in contrast to *C. cygneus* and *C. hobackensis*. P₄ differs from those of *C. cygneus* and *C. hobackensis* in having seven apical cusps on primary shearing blade and in lacking distinct posterior apical cusp on crest uniting main blade with talonid heel. P³⁻⁴ further differ from those of *C. cygneus* in having triple, rather than dual, median crests (upper teeth are unknown for *C. hobackensis*).

Etymology.—Latin *oriens*, the rising sun, east; in allusion to the complicated pattern of cusps and crests on P³⁻⁴, which vaguely recalls the rising sun, and to the discovery of this species on the Asian continent.

Description.—A partial lower dentition is preserved in near occlusion with an associated, crushed snout in the holotype, and the following description is based on this specimen unless otherwise noted (Fig. 10, 11). Although the anterior part of the dentary has suffered postmortem deformation, all mandibular tooth loci are represented, either by their crowns (P₄–M₃) or by their alveoli (loci anterior to P₄). The anteriormost alveolus is by far the largest. It clearly held the hypertrophied and procumbent I₁ in life. Between the alveolus for I₁ and the crown of P₄ there are four small alveoli, all showing

←
Fig. 11.—*Carpocristes oriens*, n. gen. and sp., holotype (part), IVPP V10697.1-2. Crushed snout preserving complete right P³ (A), left P³–M³ (P³ broken) (B), and unidentifiable right upper molars. Both views are occlusal stereopairs. Scale = 5 mm. Note inferior part of left dentary of holotype (see Fig. 10), which is visible lingual to the left maxillary tooth row in (B).

roughly the same dimensions. Presumably, *C. oriens* retained P_2 , a tooth that was seemingly lost (perhaps in parallel—see below) in both *C. cygneus* and *C. hobackensis* (Rose, 1975; Krause, 1978).

In labial outline, P_4 (L, 2.05 mm; W, 1.10 mm) is relatively low-crowned, elongated, and gently rounded, as in *C. hobackensis* and *C. cygneus* but in contrast to *Carpodaptes* and *Carpolestes* (see Rose, 1975:fig. 11). The main shearing blade supports seven small apical cusps, more than occur here in *C. cygneus* and *C. hobackensis*. As in *C. hobackensis* but in contrast to *C. cygneus*, there is only inconsequential development of vertical ribs beneath the apical cusps on the lingual side of P_4 . The posterior apical cusp of P_4 , which is well differentiated in *C. cygneus* and weakly so in *C. hobackensis*, is indistinguishable from the strong crest uniting the main blade with the talonid cusp in *C. oriens*. As in both *C. cygneus* and *C. hobackensis*, there is a well-defined posterolingual excavation on P_4 , which results in the S-shaped occlusal pattern characteristic of the shearing blade of P_4 in *Carpocristes*. The posterolingual excavation is not smoothly concave in *C. oriens*, because a vertically oriented bulge of enamel reinforces the base of P_4 in this region. A comparable swelling of enamel occurs in the posterolingual excavation on P_4 in *C. cygneus*, in which this structure clearly constitutes the base of the well-differentiated posterior apical cusp. The presence of a similar structure in *C. oriens* is probably a vestige of the posterior apical cusp of P_4 in this species.

The lower molars of *C. oriens* differ little from those of *C. cygneus* and *C. hobackensis* and will not be described in detail here. M_1 in *C. oriens* differs subtly from its homologue in North American *Carpocristes* in having a relatively shorter trigonid, although the paraconid and metaconid are as widely splayed as in the latter species. Measurements of the lower molars preserved in IVPP V10697.1-1 are as follows: M_1L , 1.05 mm; M_1W , 1.10 mm; M_2L , 0.95 mm; M_2W , 1.05 mm; M_3W , 0.95 mm (M_3L cannot be reliably measured due to breakage).

P^3 is complete but slightly worn in IVPP V10697.1-2 (L, 1.60 mm; W, 1.45 mm); this tooth is unworn but missing its anterolabial moiety in IVPP V10697.2. The labial side of P^3 bears five cusps, the first of which is displaced anteriorly and occurs in a lower occlusal plane than the remainder. In contrast, in *C. cygneus* the labial row of P^3 bears only four cusps, the anteriormost of which is relatively larger than in *C. oriens* and lies in roughly the same occlusal plane as the other labial cusps. In *C. oriens* the posterior four labial cusps decrease in size posteriorly, as is the case in *C. cygneus* (in which only three cusps occupy the same positions). A strong median cusp, probably homologous with the paraconule, is situated immediately lingual to the second labial cusp. Running in a posterolabial direction from the vicinity of the primary median cusp to the posterior margin of the tooth are three roughly parallel crests. Between these three median crests and the two subequal lingual cusps is a marked depression. A similar condition exists in *Carpodaptes* and *Carpolestes*.

P^4 (IVPP V10697.1-2: L, 1.50 mm; W, 1.40 mm; IVPP V10697.2: L, 1.40 mm; W, 1.40 mm) bears five labial cusps, the third and fourth of which are the largest and likely represent paracone and metacone, respectively. The two anteriormost labial cusps lie in a lower occlusal plane and are separated somewhat anteriorly from the remainder of the labial cusps. Between the labial and lingual rows of cusps on P^4 is a complicated system of crests and small cusps, which is similar to but more elaborate and symmetrical than that on P^3 . Directly lingual to the cusp that is thought to represent the paracone is a relatively prominent median cusp that may represent a paraconule. Crests run anterolabially and posterolabially from this primary median cusp to the anterior and posterior borders of the tooth. A second, smaller median cuspule occurs immediately posterior to the putative paraconule, on the posterior crest that emanates from it. This second median cuspule lies directly lingual to the fourth labial cusp, and may represent a small metaconule. Two further, tiny median cuspules lie on the anterior crest that stems from the putative paraconule in IVPP V10697.2. Only one of these diminutive median cuspules is apparent on the holotype, in which the other small cuspule may have been obscured by wear. Both anteriorly and posteriorly, two supplementary median crests run lingual and roughly parallel to the main crests that originate from the paraconule, producing an intricate network of triple median crests on each side of the midline of P^4 . The lingual row is dominated by the central cusp, which is probably homologous with the protocone. Accessory cuspules adorn the base of the central, lingual cusp both anteriorly and posteriorly, and both of these cuspules are situated somewhat lingual to this central cusp, as occurs variably in *Carpodaptes* (Rose, 1975:fig. 18).

The upper molars of *Carpocristes oriens* are smaller than those of any other carpolestid, but show the typical carpolestine morphology. Measurements of these teeth in IVPP V10697.1-2 are as follows: M^1L , 0.95 mm; M^1W , 1.35 mm; M^2L , 0.90 mm; M^2W , 1.45 mm; M^3L , 0.90 mm; M^3W , 1.40 mm. For the more fragmentary IVPP V10697.2 the same measurements are: M^1L , 1.00 mm; M^2L , 0.95 mm; M^3L , 0.85 mm; M^3W , 1.35 mm.

Discussion.—*Carpocristes oriens* obviously represents a much more advanced carpolestid than does *Chronolestes simul*. Indeed, its highly derived P_4 and P^{3-4} readily identify it as a nested member of the carpolestine radiation, a clade that

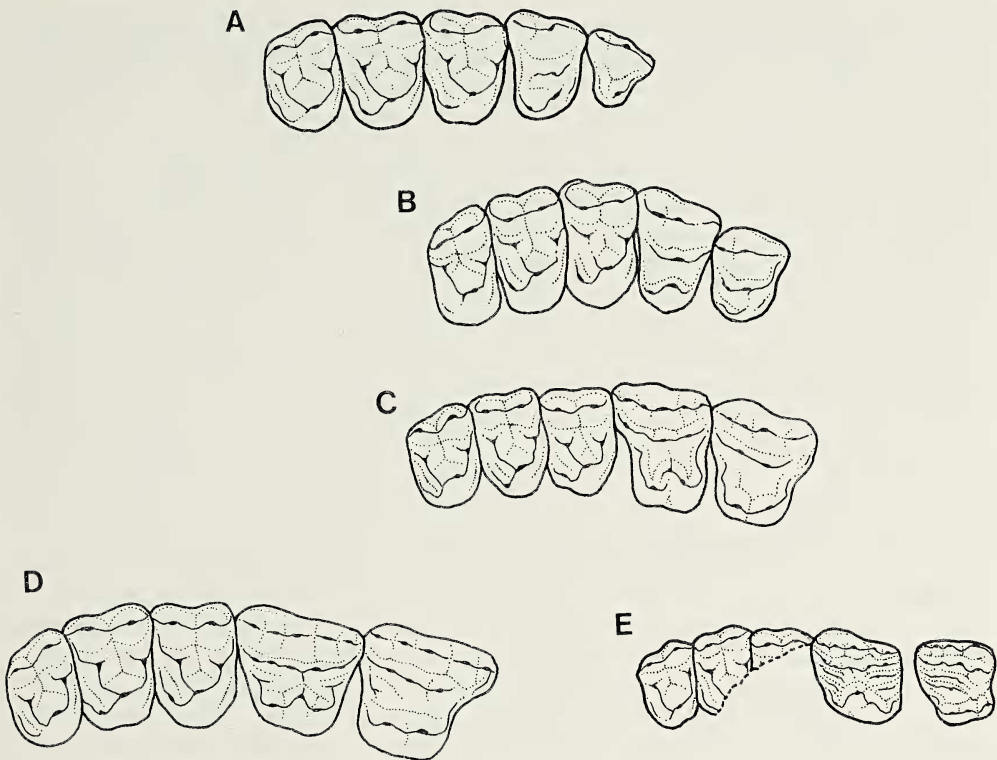


Fig. 13.—Upper cheek teeth of selected carpolestids in occlusal view, drawn at the same scale (modified after Rose, 1975:fig. 34). (A) *Chronolestes simul*; (B) *Elphidotarsius* sp., cf. *E. florencae*; (C) *Carpodaptes hazelae*; (D) *Carpolestes dubius*; (E) *Carpocristes oriens*. The sequence from A–C likely corresponds to a morphocline in terms of progressive elaboration of P^{3-4} . The alternative autapomorphous conditions exhibited by P^{3-4} in *Carpolestes* (D) and *Carpocristes* (E) may each be rooted in the more primitive conditions shown by *Carpodaptes* (C).

is otherwise restricted to North America in terms of its known geographic range (e.g., Rose, 1975; Krause, 1978; Szalay and Delson, 1979; Fox, 1984b).

Although it is now clear that the evolution of North American *Carpolestinae* was more complex than earlier views maintained (Fox, 1984b), P^{3-4} do show a general pattern of progressive morphologic complication through time among North American carpolestines. This progressive elaboration of P^{3-4} primarily entailed an increase in size associated with multiplication of cusps comprising the labial, median, and lingual rows (Rose, 1975:fig. 34). Hence, the derived and late-occurring *Carpolestes* differs from the earlier and more primitive *Elphidotarsius* chiefly in having larger P^{3-4} that bear a greater number of cusps along the labial, median, and lingual rows. A different pattern of complication of P^{3-4} , characterized by proliferation in the number of crests comprising the median row, distinguishes *Carpocristes oriens* from most North American carpolestines (Fig. 13). Accordingly, the most extreme, but morphologically divergent, specializations in P^{3-4} among carpolestids occur in *Carpolestes* and *Carpocristes*. Each of these autapomorphous conditions can be linked with more primitive character states found in species that are usually included in *Carpodaptes*.

As the genus was defined by Rose (1975), at least five species of *Carpodaptes*

existed during Tiffanian time in western North America. The upper dentition remains unknown in three of these five species, *Carpodaptes aulacodon* (the type species of the genus), *Carpodaptes jepseni*, and "*Carpodaptes*" *hobackensis* [upper dentitions referred by Holtzman (1978) to "*Carpodaptes*" *hobackensis* are not accepted as pertaining to this species here; see below]. However, variation in the morphology of P^{3-4} among the other species attributed to *Carpodaptes* is marked enough to suggest, along with aspects of P_4 morphology, that these species comprise a highly paraphyletic assemblage. Certain species, such as *Carpodaptes jepseni*, appear to share close common ancestry with *Carpolestes* (Rose, 1975), while others, particularly "*Carpodaptes*" *hobackensis* and "*Carpodaptes*" *cygneus*, seem to share more recent common ancestry with *Carpocristes*.

Unlike those of other species of North American carpolestines, P^{3-4} in "*Carpodaptes*" *cygneus* possess a second median crest, located lingual to the primary median crest found in all carpolestines. This derived pattern is especially apparent on the well-preserved specimens of "*Carpodaptes*" *cygneus* from the Roche Percée local fauna of southeastern Saskatchewan described by Krause (1978:fig. 2h-i, 3). On P^3 in "*Carpodaptes*" *cygneus* the neomorphic second crest runs parallel to the main median crest over approximately the posterior third of its course. In *Carpocristes oriens* three crests form the median row, but in both taxa the accessory median crests are limited to the posterior part of P^3 . P^4 in "*Carpodaptes*" *cygneus* possesses dual median crests both anteriorly and posteriorly, whereas triple crests occupy these positions in *Carpocristes oriens*. The distinctive and derived elaboration of median crests on P^{3-4} in "*Carpodaptes*" *cygneus* suggests that this species is closely related to *Carpocristes oriens*. This conclusion is corroborated by the structure of P_4 in *Carpocristes oriens*, "*Carpodaptes*" *cygneus*, and "*Carpodaptes*" *hobackensis*.

P_4 in *Carpocristes oriens*, "*Carpodaptes*" *hobackensis*, and "*Carpodaptes*" *cygneus* differs in several respects from its homologue in other carpolestines. In all of these species P_4 is relatively low-crowned and gently rounded in labial view, in contrast to the higher-crowned P_4 found in *Carpodaptes aulacodon*, *Carpodaptes jepseni*, *Carpolestes*, and, to a lesser extent, *Carpodaptes hazelae*. This aspect of P_4 morphology is plausibly interpreted as a primitive retention in *C. oriens*, *C. cygneus*, and *C. hobackensis* (derived in *Carpolestes* and *Carpodaptes* sensu stricto) because it resembles conditions found in *Elphidotarsius*. However, several other aspects of P_4 morphology are best interpreted as derived in species attributed here to *Carpocristes*. These include: (1) posterior displacement of posterior apical cusp of P_4 , so that this cusp is more nearly equidistant between talonid cusp and penultimate apical cusp; (2) presence of posterolingual excavation on P_4 crown, yielding S-shaped shearing blade in occlusal view; and (3) presence of more strongly defined crest uniting main shearing blade with talonid cusp. Here, these characters are interpreted as synapomorphies supporting the monophyly of *Carpocristes* (including *C. oriens*, *C. hobackensis*, and *C. cygneus*). Within *Carpocristes*, two derived P_4 characters are shared by *C. oriens* and *C. hobackensis* to the exclusion of *C. cygneus*. These include: (1) reduced development of vertical ribs beneath the apical cusps on the lingual side of P_4 ; (2) reduced expression of posterior apical cusp on P_4 , so that it is barely distinguishable (*C. hobackensis*) or indistinguishable (*C. oriens*) from the crest uniting the main shearing blade with the talonid cusp on P_4 . These characters are interpreted here as evidence that *C. hobackensis* and *C. oriens* are sister taxa. *Carpocristes cygneus* appears to be the sister group of the *C. oriens* + *C. hobackensis* clade.

Given these hypothesized relationships, it is necessary to transfer the species “*Carpodaptes*” *cygneus* and “*Carpodaptes*” *hobackensis* from *Carpodaptes* to *Carpocristes*.

Carpocristes hobackensis (Dorr, 1952), **new combination**

Carpodaptes hobackensis: Dorr, 1952:82; Rose, 1975:30; Holtzman, 1978:47 (part).

Discussion.—Confusion regarding the content, morphology, and distribution of this species stems from the misallocation of several specimens to this taxon by Holtzman (1978). These specimens, all of which are from the Tongue River Formation of western North Dakota, include the only upper dentitions ever referred to *C. hobackensis* (see Holtzman, 1978:fig. 9.4). While we agree with Holtzman that two species of carpolestids are likely to be represented by the sample from the Tongue River Formation, neither of these species appears to be *Carpocristes hobackensis* (they more likely represent *Carpocristes cygneus* and *Carpodaptes hazelae*). Accordingly, we restrict the hypodigm of *C. hobackensis* to Dorr’s (1952) original sample from Dell Creek Quarry in the Hoback Basin, western Wyoming, among which specimens preserving aspects of the upper dentition are lacking. We predict that when the upper dentition of *C. hobackensis* is finally recovered, it will possess at least as many characters in common with *C. oriens* as does *C. cygneus*.

Dell Creek Quarry is latest Tiffanian (Ti5) in age, significantly younger than the Judson and Brisbane localities in the Tongue River Formation (both of which are middle Tiffanian or Ti3; see Archibald et al., 1987) that yielded the carpolestid fossils referred by Holtzman (1978) to *C. hobackensis*. *Carpocristes hobackensis* is apparently restricted to younger strata than those bearing *C. cygneus*, which accords well with the slightly more derived P₄ anatomy of the former species.

Carpocristes cygneus (Russell, 1967), **new combination**

Carpolestes cygneus: Russell, 1967:19.

Carpodaptes cygneus: Rose, 1975:32; Krause, 1978:1253.

Carpodaptes hobackensis: Holtzman, 1978:47 (part).

Known Distribution.—Late Paleocene, middle–late Tiffanian (Ti3–Ti4) of Alberta, Saskatchewan, and North Dakota.

Discussion.—The anatomy of this species was described in detail by Krause (1978); additional records were reported by Holtzman (1978) and Fox (1990a). *Carpocristes cygneus* was apparently widely distributed in western Canada during the middle and late Tiffanian (Fox, 1990a).

DISCUSSION

Plesiadapoid Phylogeny

Many authors have noted the apparent closeness of relationship among the Plesiadapidae, Saxonellidae, and Carpolestidae (e.g., Van Valen, 1969, in press; Szalay, 1972; Rose, 1975; Szalay and Delson, 1979), and these families are often classified together as the Plesiadapoidea (Rose, 1975; Szalay and Delson, 1979; Beard, 1993a, 1993b; Van Valen, in press). However, potential synapomorphies for Plesiadapoidea have never been explicitly proposed. At least to some extent, this poor level of support for plesiadapoid monophyly may reflect our very limited knowledge of carpolestid and (especially) saxonellid anatomy. In contrast to ple-

siadapids, both skulls and postcrania of which have been known for some time (Simpson, 1935a; Russell, 1964; Szalay et al., 1975; Gingerich, 1976; MacPhee and Cartmill, 1986; Beard, 1993a), anatomical data for carpolestids and saxonellids is limited primarily to the dentition. Accordingly, morphological support for plesiadapoid monophyly must be restricted to dental characters at present. Within this limitation, however, certain dental characters do appear to bolster the hypothesis of plesiadapoid monophyly.

Szalay and Delson (1979:72), in listing dental characters that distinguish plesiadapoids from "paromomyoids," cited differences in the shape and position of the protocone on the upper molars as diagnostic for Plesiadapoidea. In plesiadapoids the upper molar protocones are nearly central in position and are weakly canted mesially, in contrast to the condition in paromomyids, micromomyids, palaechthonids, and *Purgatorius* (Kielan-Jaworowska et al., 1979:fig. 12-21; Szalay and Delson, 1979; Fox, 1984a; Beard and Houde, 1989; Gunnell, 1989). The taxonomic distribution of alternative character states suggests that the condition in plesiadapoids is derived, and we propose that centrally placed, weakly canted upper molar protocones is a synapomorphy for Plesiadapoidea. In addition, all plesiadapoids possess a distinct paraconule on P⁴. This structure is absent on P⁴ in paromomyids, micromomyids, palaechthonids, and *Purgatorius*, and is therefore a second potential dental synapomorphy for Plesiadapoidea.

Relationships within Plesiadapoidea are more hotly contested than the monophyly of the group at present. Russell (1964) originally described *Saxonella* as a member of the Carpolestidae, but, as recently summarized by Fox (1991), few subsequent authors have favored a special relationship between carpolestids and saxonellids to the exclusion of plesiadapids. Instead, many workers have viewed saxonellids and carpolestids as independently autapomorphous descendants of relatively unspecialized plesiadapids. Van Valen (1969) expressed this viewpoint as follows:

As shown by all the known anatomy of *Elphidotarsius* and *Saxonella*, supplemented by that of later carpolestids, the Carpolestinae and Saxonellinae of Russell (1964) were derived from the Plesiadapidae. It is furthermore evident from the non-homology of the slicing teeth in the Carpolestinae and Saxonellinae that they had separate origins from *Pronothodectes* or just possibly some unknown more primitive plesiadapid. The carpolestids are here given family rank only because they became sufficiently specialized, more so than *Saxonella*, before their extinction (Van Valen, 1969:295).

Hence, Van Valen's attribution of *Saxonella* to the Plesiadapidae reflected his view that *Saxonella* is phenetically less distant from plesiadapids than are carpolestids. Importantly, Van Valen (1969) made no claim regarding the relative recency of common ancestry among carpolestids, plesiadapids, and saxonellids. Szalay and Delson (1979:91) went beyond Van Valen (1969) in arguing for a sister group relationship between saxonellids and plesiadapids, exclusive of carpolestids. However, Szalay and Delson (1979) failed to discuss potential synapomorphies for their Saxonellidae + Plesiadapidae clade, and other workers have doubted its validity (e.g., Gingerich, 1976; Fox, 1991; Van Valen, in press).

Chronolestes provides new insight into the relationships among plesiadapoid families because it significantly alters our conception of dental morphology in primitive carpolestids. If we are correct in interpreting *Chronolestes* as a basal carpolestid (see below), the dentition of early carpolestids must have been more

primitive in several respects than that of any plesiadapid or saxonellid discovered to date. Accordingly, several characters that were previously thought to be universally distributed among plesiadapoids now appear to be more readily interpreted as synapomorphies of a Plesiadapidae + Saxonellidae clade. These characters include: (1) presence of distinct metacone on P^{3-4} , (2) presence of distinct paraconule on P^3 , (3) P^3 protocone higher and more conical than in *Chronolestes*, and (4) presence of at least a weak parastyle on P^{3-4} (autapomorphously enlarged on P^3 in *Saxonella*). As Fox (1993) has recently demonstrated, primitive carpoolestids further differ from known plesiadapids and saxonellids in retaining a more primitive dental formula, and it is possible that the reduced dental formulae of plesiadapids and saxonellids are also partly homologous.

Carpolestid Phylogeny

Chronolestes simul differs rather dramatically from carpoolestines in lacking a polycuspidate, bladelike P_4 and in having much simpler I^1 and P^{3-4} . Given that the plagiaulacoid structure of P_4 and correlated specializations of P^{3-4} in carpoolestids have often been portrayed as the defining characteristics of the family (Simpson, 1935b; Szalay, 1972; Rose, 1975; Szalay and Delson, 1979), our reasons for assigning *Chronolestes* to the Carpoolestidae must be spelled out explicitly.

As in all plesiadapoids, the upper molars of *Chronolestes* possess protocones that are nearly central in position and weakly canted mesially. P^4 in *Chronolestes* possesses a distinct paraconule, as do those of all other plesiadapoids. Hence, *Chronolestes* possesses both of the dental synapomorphies cited previously as supporting the monophyly of plesiadapoids, and its attribution to this clade seems beyond reasonable doubt. Further derived features of the dentition of *Chronolestes* strongly point toward carpoolestid affinities for this taxon, because all of these traits also occur in carpoolestines (although sometimes in a more highly transformed state) and because crossing synapomorphies are as yet unknown. The following dental traits are shared by *Chronolestes* and carpoolestines to the exclusion of plesiadapids and saxonellids, and appear to be synapomorphies of the Carpoolestidae as the taxon is used in this paper: (1) P_3 highly reduced, (2) P_4 strongly hypertrophied (both in terms of crown height and mesiodistal elongation), (3) P_4 exodaenodont, and (4) P_4 with distinct metaconid. Dental synapomorphies characterizing carpoolestids other than *Chronolestes* were listed in the subfamilial diagnosis for Carpoolestinae above.

A reconstruction of phylogenetic relationships among selected plesiadapoids based on a cladistic analysis of dental characters is depicted in Fig. 14 (also see appendices 1–2).

Relationships of Altanius orlovi

Altanius orlovi is an interesting primate of uncertain phylogenetic position, known only from the Bumban Member of the Naran Bulak Formation in the Nemegt Basin of southern Mongolia (Dashzeveg and McKenna, 1977; Gingerich et al., 1991). The associated mammalian fauna suggests an early Eocene (Bum-banian) age for *Altanius* (Russell and Zhai, 1987). Hence, *Altanius* seems to be very close in age to *Chronolestes simul* and *Carpocristes oriens* from Wutu (see also Tong and Dawson, 1995).

Altanius was initially described as an anaptomorphine omomyid most closely similar to the North American early Eocene genera *Anemorhysis*, *Tetonius*, and *Pseudotetonius*, although similarities to the primitive carpoolestine *Elphidotarsius*

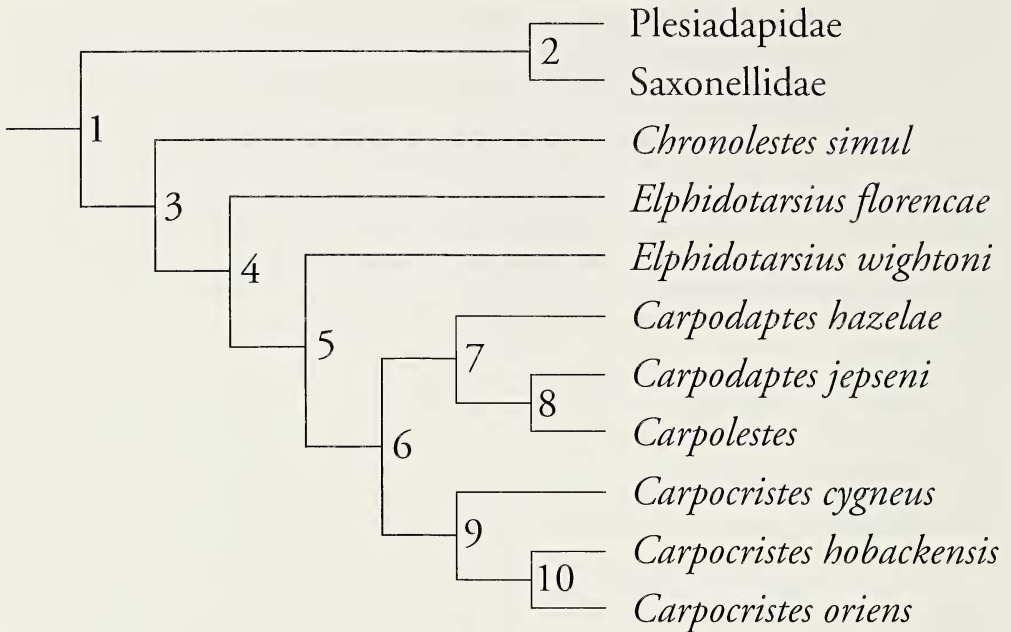


Fig. 14.—Hypothesis of phylogenetic relationships among selected plesiadapoids based on dental characters (see Appendices 1–2). Trees were rooted by designating a hypothetical ancestor (in which all characters were scored as “0”) as the outgroup to all plesiadapoid taxa. Using the branch-and-bound algorithm in PAUP 3.0s (Swofford, 1990), the taxon-character matrix shown in Appendix 2 yielded a single most parsimonious tree, which is illustrated here (tree length = 46, consistency index = 0.848).

Synapomorphies supporting each node are as follows (unambiguous synapomorphies, or those that support a node regardless of optimization algorithm, are indicated by the abbreviation U; ambiguous synapomorphies, which support a node only under certain optimization algorithms, are identified as AD and AA to distinguish ambiguous synapomorphies collected under DELTRAN or ACCTRAN optimizations, respectively): Node 1 (Plesiadapoidea), U26 0>>1, U27 0>>1, AA10 0>>1; Node 2 (Plesiadapidae + *Saxonella*), U1 0>>1, U2 0>>1, U3 0>>1, U4 0>>1, U5 0>>1, AD10 0>>1; Node 3 (Carpolestidae), U6 0>>1, U7 0>>1, U8 0>>1, U9 0>>1; Node 4 (Carpolestinae), U4 0>>2, AA11 0>>1, U12 0>>1, U13 0>>1, U14 0>>1, U23 0>>1; Node 5 (*Elphidotarsius wightoni* + *Carpodaptes* + *Carpolestes* + *Carpocristes*), U12 1>>2, U25 0>>1; Node 6 (*Carpodaptes* + *Carpolestes* + *Carpocristes*), AD10 0>>1, AD11 0>>1, U12 2>>3, U14 1>>2, U15 0>>1, U23 1>>2; Node 7 (*Carpodaptes* + *Carpolestes*), U22 0>>1, U24 0>>1; Node 8 (*Carpodaptes jepseni* + *Carpolestes*), U22 1>>2, AD23 2>>3; Node 9 (*Carpocristes*), U13 1>>2, U16 0>>1, U17 0>>1, U18 0>>1, U21 0>>1, AD23 2>>3; Node 10 (*Carpocristes hobackensis* + *Carpocristes oriens*), AA12 3>>4, AA13 2>>3, U19 0>>1, U20 0>>1.

were also noted (Dashzeveg and McKenna, 1977). Subsequently, Rose and Krause (1984) reassessed the relationships of *Altanius*, concluding that “The comparisons presented here, rather than confirming omomyid affinity, suggest an alternative possibility—that *Altanius* may be a conservative, archaic plesiadapiform derived from a form similar or ancestral to *Elphidotarsius*, but with a more primitive P₄ that had not achieved the hypertrophy and polycuspidation characteristic of *Elphidotarsius*” (Rose and Krause, 1984:725). This interpretation of the phylogenetic position of *Altanius* has not been widely accepted (Szalay and Li, 1986; Gingerich et al., 1991), however, and more nearly complete fossils led Gingerich et al. (1991) to interpret *Altanius* as a basal euprimate (i.e., lying outside the clade including *Cantius* and *Teilhardina*).

The discovery of *Chronolestes* permits further appraisal of the Rose/Krause hypothesis concerning the phylogenetic position of *Altanius*, because *Chronolestes* is considerably more primitive than *Elphidotarsius* in ways that should approximate conditions in *Altanius* if the Rose/Krause hypothesis is correct. In our opinion, the dentition of *Chronolestes* provides no evidence to support a special relationship between carpolestids and *Altanius*. In contrast to *Altanius*, *Chronolestes* possesses characteristically carpolestid-like specializations of the lower premolars (albeit in rudimentary form): P_3 is highly reduced and P_4 is hypertrophied and exodaenodont. The anterior lower dentition of *Altanius*, as inferred from alveoli (see Gingerich et al., 1991:fig. 1C–D), also contrasts strongly with that in *Chronolestes*: I_{1-2} in *Altanius* are small (much smaller than C_1) and nearly vertically implanted, P_1 is primitively retained, and P_2 is primitively double-rooted, all in contrast to more derived conditions in *Chronolestes*. Indeed, *Altanius* lacks the synapomorphies characteristic of all plesiadapoids (centrally placed upper molar protocones that are weakly canted mesially, paraconule on P^4), which strongly implies that *Altanius* lies outside the plesiadapoid clade. Accordingly, dental similarities between *Altanius* and carpolestids cited by Rose and Krause (1984) are most plausibly interpreted as convergences. We concur with Gingerich et al. (1991) that *Altanius* is likely to be a basal euprimate.

Carpolestid Biogeography and Dispersal

The unexpected discovery of carpolestids in Asia forces us to reconsider aspects of intercontinental mammalian dispersal between Asia and North America during the Paleocene, because the North American record of Carpolestidae is restricted to this epoch (Rose, 1975, 1977, 1981; Archibald et al., 1987). Relevant issues include the timing of episodes of intercontinental mammalian dispersal between North America and Asia during the Paleocene, and the direction(s) whereby such dispersal occurred. It is assumed on paleogeographic criteria that dispersal of Paleocene mammals between Asia and North America took place across Beringia, with a less likely alternative corridor corresponding to the modern Aleutian island chain (e.g., McKenna, 1983).

The timing of episodes of intercontinental mammalian dispersal between Asia and North America during the Paleocene remains poorly constrained, primarily because of difficulties in precisely correlating Paleocene faunas on the two continents (Archibald et al., 1987; Russell and Zhai, 1987). Sloan (1987) suggested that mammalian dispersal between Asia and North America occurred at frequent (and strictly delimited) intervals during the Paleocene, but in some cases his interpretations are based on inadequately corroborated hypotheses of phylogenetic relationships and/or poorly documented assessments of age. Despite Sloan's assertions, there is little consensus at present concerning the exact timing of mammalian dispersal between Asia and North America during the Paleocene. Perhaps the only exception to this rule relates to the apparently synchronous appearance in North America of several higher-level taxa of mammals, including the orders Rodentia and Tillodontia and the pantodont family Coryphodontidae, at the beginning of the Clarkforkian Land Mammal Age. This major episode of mammalian immigration into North America is widely interpreted as the result of dispersal of rodents, tillodonts, and coryphodontids across Beringia from Asia (Rose, 1981; Krause and Maas, 1990).

Although evidence is less conclusive than for the basal Clarkforkian, it is clear that earlier episodes of trans-Beringian mammalian dispersal also occurred during the Paleocene. Interestingly, a significant episode of trans-Beringian dispersal

seems to have only slightly preceded the well-documented basal Clarkforkian event, occurring in latest Tiffanian zone Ti5. In North America this interval is marked by the first appearance of the order Dinocerata (e.g., Thewissen and Gingerich, 1987) and the family Arctostylopidae (Cifelli et al., 1989), both of which were likely immigrants from Asia at this time (Schoch and Lucas, 1985; Cifelli et al., 1989; contra Gingerich, 1985). A considerably earlier interval of trans-Beringian dispersal, corresponding to middle Torrejonian or earlier time, is marked by the first appearance (To3) of the order Pantodonta (*Pantolambda*) in North America (probably as an immigrant from Asia; but see de Muizon and Marshall, 1992) and by dispersal of the *Sphenopsalis* + *Prionessus* + *Lambdopsalis* clade of taeniolabidid multituberculates to Asia from North America (Simmons and Miao, 1986). Other intervals of trans-Beringian dispersal of mammals during the Paleocene are also possible (Sloan, 1987), but these remain poorly documented at present.

How does the newly discovered carpolestid record of Asia compare with this pattern of trans-Beringian mammalian dispersal during the Paleocene? The phylogenetic positions of the Wutu carpolestids constrain the timing of carpolestid dispersal events across Beringia, but these constraints are dependent on assumptions concerning the relative completeness of the North American and Asian fossil records.

For example, the first appearance of *Elphidotarsius* (and of the subfamily Carpolestinae) in North America occurs in late Torrejonian zone To3 (Archibald et al., 1987). Accordingly, the cladistic branching between Chronolestinae and Carpolestinae antedates zone To3 by some unknown interval of time. Dispersal of ancestral chronolestines to Asia from North America prior to zone To3 is consistent with the absence of Chronolestinae in the North American fossil record, but implies that this clade has a long, undocumented fossil record in Asia spanning the interval from middle Paleocene to early Eocene time. Alternatively, one could minimize the inferred incompleteness of the Asian fossil record by positing a much younger date of dispersal for chronolestines to Asia from North America, but this has the disadvantage of implying that chronolestines inhabited North America for a significant part of the Paleocene without leaving behind a fossil record. Most authorities would probably agree that the North American Paleocene fossil record is currently much more nearly complete than its Asian counterpart, so we hypothesize that Chronolestinae likely dispersed to Asia from North America prior to zone To3. This timing conforms remarkably well with the earlier interval of trans-Beringian Paleocene mammalian dispersal discussed above (Fig. 15). We favor dispersal of Chronolestinae to Asia from North America over dispersal of Carpolestinae in the opposite direction because outgroups to Carpolestidae (Plesiadapidae, Saxonellidae, Eudermoptera) are known in North America but have not yet been found in Asia.

Carpocristes cygneus, the oldest species currently attributed to this genus, first appears in the fossil record in middle Tiffanian zone Ti3 in Alberta (Fox, 1990a), but is known best from slightly younger (Ti4) localities in Alberta, Saskatchewan, and North Dakota (Krause, 1978; Holtzman, 1978; Fox, 1990a). The dentally more advanced species *Carpocristes hobackensis* is known with certainty only from the latest Tiffanian (Ti5) Dell Creek Quarry, Hoback Basin, Sublette County, Wyoming (Dorr, 1952). Both North American species of *Carpocristes* are apparently older than *Carpocristes oriens* from Wutu, which accords well with their more primitive dental morphology. Consequently, we favor dispersal of the *Car-*

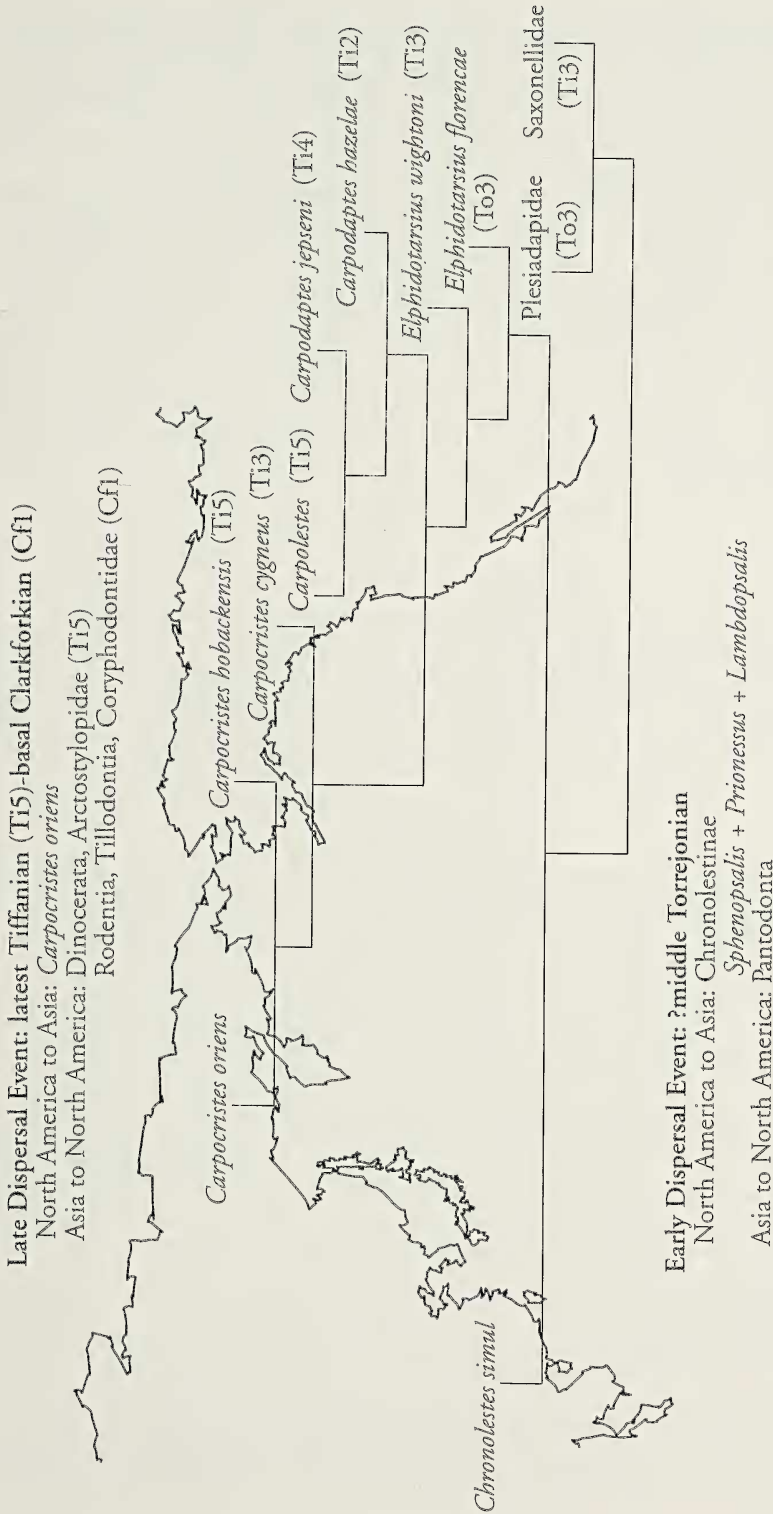


Fig. 15.—Cladogram illustrating phylogenetic relationships among plesiadapoids (from Fig. 14) superimposed on a map of Asia and North America to reflect known geographic occurrences of taxa (at continental scale only). Earliest known biostratigraphic occurrences for North American taxa are shown in parentheses. At least two trans-Beringian dispersal events for carpodlestids are required to reconcile their known geographic occurrences with the phylogenetic reconstruction shown in Figure 14. Our preferred hypothesis concerning the timing and direction of carpodlestid dispersal agrees with estimates concerning the timing of trans-Beringian dispersal of other groups of Paleocene mammals.

pocristes oriens lineage from North America to Asia no earlier than zone Ti5. The timing of this hypothesized dispersal event compares favorably with both the Ti5 and the basal Clarkforkian mammalian interchanges across Beringia noted above. Given the weak temporal constraints provided by the current paleontological data, we make no attempt to endorse either of these intervals as the more likely time for trans-Beringian dispersal of the *Carpocristes* lineage (Fig. 15).

Obviously, our preferred hypotheses for trans-Beringian dispersal of carpoles-tids may be refuted or refined by future paleontological discoveries in Paleocene strata of Asia and North America. One factor that must be borne in mind in this regard is the paucity of data regarding higher latitude Paleocene mammal localities on both continents. For example, Fox's (1984*b*, 1990*b*, 1991) recent discoveries of carpoles-tids and other plesiadapoids in Alberta suggest that at least some species were restricted to more northerly regions in North America. This strong potential for geographical bias in fossil preservation and/or recovery may well have skewed current concepts regarding the true spatiotemporal distributions of carpoles-tids and their close relatives.

Carpoles-tid Extinction

Chronolestes simul and *Carpocristes oriens* are associated with the perissodactyl *Homogalax* and a new genus and species of artiodactyl at Wutu. These taxonomic associations have never been encountered in the North American fossil record, where carpoles-tids became extinct by the end of Clarkforkian time and perisso-dactyls and artiodactyls first appeared at the base of the Wasatchian (Rose, 1975, 1980, 1981; Maas et al., 1988; Gingerich, 1989; Krause and Maas, 1990). Cor-relation of faunas representing the Bumbanian Land Mammal Age in Asia (among which the Wutu fauna must now be considered a primary example) relative to the Clarkforkian-Wasatchian boundary in North America has only been estimated via biostratigraphy based on the fossil mammals themselves (e.g., Rose, 1980, 1981; Dashzeveg, 1982, 1988; Krause and Maas, 1990), leading to obvious prob-lems of circularity if one's goal is to assess the relative ages of the mammalian faunas (e.g., Wing, 1984; Krause and Maas, 1990). The unique taxonomic asso-ciation of carpoles-tids, perissodactyls, and artiodactyls at Wutu can be interpreted in either of two ways: (1) the Wutu carpoles-tids are the youngest carpoles-tids in the fossil record, having persisted into the early Eocene; or (2) the Wutu carpo-les-tids are no younger than North American carpoles-tids, but the associated arti-odactyl and *Homogalax* are older (i.e., Paleocene) than all records of these taxa in North America and Europe. Until more convincing evidence is available that at least some early Asian perissodactyls and artiodactyls are older than the basal Wasatchian/Sparnacian, we tentatively interpret the Wutu carpoles-tids as the youngest representatives of that clade. The problem of correlating Bumbanian faunas in Asia with Wasatchian/Sparnacian faunas in North America and Europe deserves a great deal of additional study, but this is obviously beyond the scope of this paper.

In North America the extinction of carpoles-tids occurred soon after the suc-cessful colonization of the continent by rodents. Citing several different lines of evidence, Maas et al. (1988) suggested that the extinction of North American carpoles-tids may have resulted from competitive displacement by rodents. Prom-inent among the lines of evidence marshalled by Maas et al. (1988) in support of this hypothesis were the patterns of paleobiogeographic distribution then known for carpoles-tids and rodents. That is, rodents were acknowledged as having orig-

inated in Asia (e.g., Li et al., 1987; Dashzeveg and Russell, 1988), developing competitively superior adaptations allopatrically from North American carpoles-tids that allowed competitive displacement of carpoles-tids by rodents after dispersal of the latter across Beringia at the beginning of Clarkforkian time.

The new evidence regarding early Cenozoic Asian carpoles-tids reported here calls this hypothesis into question. At Wutu, *Chronolestes simul* and *Carpocristes oriens* occur in association with a surprising diversity of rodents, including representatives of Paramyidae, Alagomyidae, and Ctenodactyloidea (Tong and Dawson, 1995). Furthermore, if the hypotheses for trans-Beringian carpoles-tid dispersal discussed previously are accurate, carpoles-tids were present in Asia for a large part of Paleocene time (perhaps since the middle Torrejonian). Over this interval Asian carpoles-tids would likely have coexisted with at least some early rodents and their close relatives, since Asia seems to have been the continent on which this order originated. If rodents caused the extinction of North American carpoles-tids through competitive exclusion, the same pattern should hold in Asia. That two clades of carpoles-tids were able to successfully colonize Asia at the same time that rodents were undergoing their initial evolutionary radiation there forces us to reconsider the causes of carpoles-tid extinction on both continents.

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APPENDIX 1

CHARACTER DESCRIPTIONS

The following dental characters formed the basis for a cladistic analysis, the results of which are illustrated in Fig. 14. Characters were polarized using *Purgatorius*, *Paromomys*, and *Micromomys* as outgroups. Primitive states for each character are coded as “0”, while derived states are coded as positive integers. Multistate characters were treated as “unordered” for purposes of parsimony analysis, unless otherwise noted.

1. P³ metacone absent (0), or present (1).^a
2. P³ paraconule absent (0), or present (1).^a
3. P⁴ metacone absent (0), or present (1).^a
4. P³ protocone weak (0), higher and more bulbous (1), or weak and closely followed by a crest or second lingual cusp (2).
5. P³ parastyle absent (0), or present (1).^a
6. P₃ unreduced (0), or reduced (1).
7. P₄ not hypertrophied (0), or hypertrophied in terms of both mesiodistal elongation and enhanced crown height (1).
8. P₄ not exodaenodont (0), or exodaenodont (1).
9. P₄ metaconid absent (0), or present (1).
10. I¹ “laterocone” or “disto-apical cusp” absent (0), or present (1).
11. I¹ mesio-basal cusp absent (0), or present (1).
12. Number of cusps in buccal row of P³ = one (0), two (1), three (2), four (3), or five (4).^{b,c}
13. Number of median crests on P³⁻⁴ = none (0), one (1), two (2), or three (3).^{b,c}
14. Number of cusps in buccal row of P⁴ = one (0), four (1), or five (2).^{b,c}
15. Number of cusps in lingual row of P⁴ = one (0), or three (1).
16. Size of upper and lower molars larger than in *Carpocristes* spp. (0), or as in *Carpocristes* spp. (1).
17. Posterolingual excavation on P₄ absent (0), or present (1).
18. Posterior apical cusp of P₄ near penultimate apical cusp (0), or more posterior in position, lying roughly equidistant between penultimate apical cusp and talonid cusp (1).^c
19. Posterior apical cusp of P₄ cuspsate (0), or indistinct/absent, being incorporated within crest uniting main shearing blade of P₄ with talonid cusp (1).^c
20. Vertical ribs beneath apical cusps on lingual side of P₄ strong (0), or weak (1).^c

21. Crest uniting main shearing blade with talonid cusp of P_4 weak (0), or strong (1).^c
22. Outline of P_4 in labial view relatively low-crowned and gently rounded (0), higher-crowned but still gently rounded (1), or very high-crowned and more pointed (2).^{b,c}
23. Number of apical cusps on P_4 = two (0), four (1), five (2), six (3), seven (4), or eight (5).^{b,c}
24. P_2 present (0), or absent (1).^d
25. M_1 paraconid not widely splayed anteriorly with respect to metaconid (0), or widely splayed (1).
26. Upper molar protocones mesial in position and strongly canted mesially (0), or central in position and weakly canted mesially (1).
27. P^4 paraconule absent (0), or present (1).

^a Character scored as missing data (?) in some or all carpolesines to reflect their highly transformed anatomy, thus assuming no homology with derived conditions; see Appendix 2.

^b Multistate character treated as "ordered" for purposes of parsimony analysis.

^c Character scored as missing data (?) in some or all non-carpolesine taxa to reflect the highly transformed anatomy of carpolesines, thus assuming no homology with derived conditions; see Appendix 2.

^d Character treated as irreversible for purposes of parsimony analysis.

APPENDIX 2

TAXON-CHARACTER MATRIX USED IN PARSIMONY ANALYSIS

Ancestor	00000	00000	00000	00000	00000	00
Plesiadapidae	11111	00001	0???0	00????	???00	11
<i>Saxonella</i>	11111	00001	0???0	00????	???10	11
<i>Chronolestes simul</i>	00000	11110	00000	0000?	0?000	11
<i>Elphidotarsius</i> sp., cf. <i>E. florencae</i>	???20	1111?	?1110	00000	00100	11
<i>Elphidotarsius</i> <i>wightoni</i>	???2?	1111?	?2110	00000	00111	11
<i>Carpodaptes haze-</i> <i>lae</i>	???2?	11111	13121	00000	01211	11
<i>Carpodaptes jepseni</i>	?????	?111?	?????	00000	023?1	??
<i>Carpolestes</i>	???2?	1111?	?3121	00000	02511	11
<i>Carpocristes cyg-</i> <i>neus</i>	???2?	11111	13221	11100	10311	11
<i>Carpocristes hob-</i> <i>ackensis</i>	?????	1111?	?????	11111	10311	??
<i>Carpocristes oriens</i>	???2?	1111?	?4321	11111	10401	11